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The American Midland Naturalist

Devoted to Natural History, Primarily
that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.



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No. 2

Taxonomic and Ecological Studies of Eastern Tennessee Bryophytes¹

Aaron J. Sharp

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¹ Papers from the Department of Botany, The Ohio State University, No. 407, and Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 31. This paper represents a major portion of the dissertation offered as a partial requirement for the doctorate degree from The Ohio State University.

1. Introduction

A. HISTORY OF BRYOLOGY IN TENNESSEE

In 1856 Sullivant recorded three species of bryophytes from eastern Tennessee. Between 1856 and 1929, additional species were recorded by Sullivant and Lesquereux (1865), Howe (1896), Evans (1897, 1905, 1910a, 1910b, 1910c, 1922), Haynes (1916), Andrews (1921), and Grout (1928) in the first installment of his "Moss Flora." In these twelve papers published prior to 1929 only fifty-four species of bryophytes were reported as definitely occurring in eastern Tennessee.

Since September, 1929, the writer has been engaged continually in the studies here presented. During that period, however, several papers mentioning Tennessee bryophytes were published by him and others. Various parts of Grout's "Moss Flora" (1928, et seq.) include data pertinent to this State. Cain (1935) published a list of species found in the spruce-fir forests of the Great Smoky Mountains. Wingo (1936) prepared annotated keys to the Tortulaceae of Tennessee and Morrison (1938) completed similar studies for the Tennessee Lejeuneae. Cain and Sharp (1938) and Billings and Drew (1938) published ecologic studies of certain Tennessee bryophytes. The author issued eleven brief contributions to the bryology of eastern Tennessee.

B. METHODS OF STUDY

The most important collection of Tennessee bryophytes previous to 1929 was that described by Andrews (1921). There was also present in the herbarium of The University of Tennessee a small collection of miscellaneous bryophytes brought together by the members of the botanical staff. Since 1929 a consistent effort was made by the members of this staff and particularly the writer to collect the bryophytes of eastern Tennessee. Because The University of Tennessee is located in the eastern part of the State, very few collections were made west of Cheatham County. Therefore, no consistent reference to that part of the State is included in the present study.

Notes of a taxonomic and ecologic nature were made either in the field as the plants were collected or later in the laboratory. Usually an attempt was made to identify the material while it was still fresh. All collections were dried, prepared for, and deposited in the herbarium. Doubtful material was submitted to specialists for identification.

Prior to the disastrous fire of January 18, 1934, which destroyed the herbarium, about three thousand packets of Tennessee bryophytes had been deposited there. Since then about four thousand packets of Tennessee material have been incorporated in the new herbarium.

Fortunately a relatively complete and annotated list of Tennessee bryophytes was saved from the fire. In addition, duplicate specimens of many Tennessee bryophytes collected both before and since the fire were deposited by the writer in other herbaria. Liverworts were sent chiefly to Yale University and The University of Cincinnati, whereas duplicates of all collections of Sphagnaceae and of many Bryaceae were sent to Dr. A. L. Andrews, Ithaca, N. Y.

Manuscript
8.31.1939

Many of the moss collections are represented in the private herbaria of Mr. E. B. Bartram, Bushkill, Pa., and Dr. A. J. Grout, Newfane, Vt., and in the herbarium of the New York Botanical Garden.

Data for the discussion of the geographical distribution of certain Southern Appalachian bryophytes were obtained by visiting various large herbaria (listed in the following section) where pertinent exsiccata were examined; other specimens were borrowed from the New York Botanical Garden.

C. ACKNOWLEDGMENTS

The writer is indebted to Dr. G. W. Blaydes and Dr. E. N. Transeau of The Ohio State University for many suggestions and criticisms. To the past and present members of the Botany Department of The University of Tennessee, thanks are due for continual aid in collecting bryophytes. Dr. A. L. Andrews, Mr. E. B. Bartram, Dr. A. W. Evans, Dr. Margaret Fulford, Dr. A. J. Grout, Miss C. C. Haynes, Dr. G. E. Nichols, Dr. W. C. Steere and Mr. R. S. Williams have assisted with the determination of difficult forms and given other valuable advice. Dr. H. C. Bold, Dr. S. A. Cain, Dr. W. H. Camp, and Dr. L. R. Hesler have advanced valuable criticisms. Phytogeographical information not available to the writer was given him by Dr. L. E. Anderson and Mr. R. T. Wareham. Dr. George M. Hall contributed certain necessary geological information.

The geographical studies could not have been complete without a grant-in-aid from the Sigma Xi Society which enabled the writer to visit the herbaria of Mr. E. B. Bartram and Dr. A. J. Grout, and the herbaria of Duke University, Harvard University, University of Michigan, Missouri Botanical Garden, New York Botanical Garden, University of Pennsylvania, Philadelphia Academy of Sciences, U. S. National Museum, and Yale University. To the curators and other botanists consulted, the writer is indebted.

2. Taxonomic Studies

A. INTRODUCTION

As noted previously no comprehensive reports of eastern Tennessee bryophytes have been published. In the following list, therefore, are included all the described species of bryophytes which are known from eastern Tennessee. Brief notes are given for each species relative to the habitats, the comparative frequency, the distribution by counties and other taxonomic or morphological information. An asterisk (*) marks the counties in which a given species was collected prior to but not since the destruction of the herbarium of The University of Tennessee on January 18, 1934. The position of the counties within the area is shown in Fig. 1.

The arrangements of the classes adopted in the list follows that of Schaffner (1938a). The organization of the *Hepaticae* is similar to that of Haynes and Evans (1925) with minor variations. Andrews (1913) was followed in listing the *Sphagneae*. The arrangement of the orders in the *Odontocarpae* (formerly called *Bryales*) is that of Schaffner (1938b). The position of the families and of the genera within the families is based in part on the writer's own views. The classes, *Schizocarpae* (*Andreaeae*) and *Anthocerotae*, are represented by one and two genera respectively in Tennessee.

At present the annotated list contains four hundred and twenty-six species of bryophytes; one or more species not reported before are usually found on each field excursion.

Keys to classes, orders, families, genera, and species are included with the hope that they may prove useful. However, they were constructed without serious consideration of the species found outside the area, and obviously will be of limited value elsewhere.

B. ANNOTATED LIST OF SPECIES WITH KEYS

KEY TO CLASSES

1. Gametophyte thalloid or leafy, with more than one chloroplast per cell; sporophyte with a spherical or ellipsoidal capsule 2
1. Gametophyte always thalloid, with but a single chloroplast per cell; sporophyte with a cylindrical capsule V. ANTHOCEROTAE
2. Gametophyte thalloid, or if leafy the capsule-wall nearly always dehiscing into 4 or more valves; rhizoids unicellular I. HEPATICAE
2. Gametophyte leafy; capsule-wall dehiscing irregularly, or by 4 longitudinal slits, or by the formation of an operculum; rhizoids multicellular 3
3. Gametophyte pale green when moist to nearly white when dry, variously tinged with red, brown or yellow; leaf with large, empty cells surrounded by small chlorophylliferous ones; sporophyte on a pseudopodium; capsule with an operculum II. SPHAGNEAE
3. Gametophyte green (seldom pale) to almost black; cell arrangement of leaf not as above 4
4. Gametophyte dark green or brown, growing only on non-calcareous rocks; sporophyte on a pseudopodium; capsule opening by 4 longitudinal slits III. SCHIZOCARPAE (ANDREAEAE)
4. Gametophyte light green to black, growing on various substrata; sporophyte never on a pseudopodium; capsule dehiscing irregularly or more frequently by the formation of an operculum IV. ODONTOCARPAE

Class I. HEPATICAE¹

KEY TO ORDERS

1. Gametophyte leafy IV. JUNGERMANNIALES
1. Gametophyte thalloid (except in *Fossombronina* which has two rows of obliquely-inserted leaves, violet rhizoids, and grows prostrate on the soil). 2
2. Sporophyte and sex-organs borne in specialized balloon-like sacs. II. SPHAEROCARPALES
2. Sporophyte and sex-organs not borne in specialized balloon-like sacs 3
3. Thallus usually 10-25 cells in thickness and more or less differentiated internally I. MARCHANTIALES
3. Thallus thin (usually less than 10 cells in thickness), and relatively undifferentiated internally III. METZGERIALES

Order I. MARCHANTIALES

KEY TO FAMILIES

1. Sporophyte, consisting of capsule only, enclosed within the thallus at maturity I. RICCIACEAE
1. Sporophyte, differentiated into capsule, stalk, and foot, maturing on specialized, elevated branches 2
2. Areolae of dorsal surface of thallus present but indistinct; air chambers in

² Keys and descriptions for all the thalloid liverworts in North America are given by Frye and Clarke (1937). Evans and Nichols (1908) formulated keys for many of the liverworts in eastern North America. A checklist (Buch, Evans and Verdoorn, 1937) for North American and European hepatics has recently appeared.

In the present paper, references are given to such monographs and other publications as describe most of the North American species of a genus.

Since the completion of this manuscript Evans has published a treatise on the phylogeny of the Hepaticae (Bot. Rev. 5:49-96. 1939.).

several layers; capsule-wall cells without semi-annular thickenings; wall not dehiscing into valves II. REBOULIACEAE

2. Areolae of dorsal surface of thallus distinct; air-chambers in a single layer; capsule-wall cells with semi-annular thickenings, wall dehiscing into irregular valves III. MARCHANTIACEAE

I. RICCIACEAE

KEY TO GENERA

1. Epidermis of the thallus without specialized pores 1. RICCIA
1. Epidermis of the thallus with distinctly differentiated pores 2. RICCIOCARPUS

1. *Riccia* L.

1. Thallus slender, floating in water or growing on wet soils; capsule borne in a protuberance on the lower side of the thallus 3. *fluitans*
1. Thallus broader, not aquatic, usually growing on drier soils; capsule borne within the thallus 2
2. Margin of thallus not ciliate 1. *arvensis*
2. Margins of thallus with stout cilia 2. *Beyrichiana*

1. *Riccia arvensis* Aust. On dry soil in small cedar barren. Rare. Knox County. There is little doubt about the identity of this plant, although the late Dr. M. A. Howe in a letter said, "—probably *R. arvensis*."

2. *Riccia Beyrichiana* Hampe. On moist soil. Rare. Blount County.

3. *Riccia fluitans* L. On moist alluvial soils. Rare. Blount and Johnson Counties.

2. *Ricciocarpus* Corda

Ricciocarpus natans (L.) Corda. Floating in backwater along streams. Rare. *Davidson County.

II. REBOULIACEAE

KEY TO GENERA

1. Sporophyte surrounded by a distinct pseudo-perianth, the latter divided longitudinally into eight segments 3. ASTERELLA
1. Sporophyte not surrounded by distinct pseudo-perianth 2
2. Thallus with bleached, ventral scales which project far beyond the margin 1. GRIMALDIA
2. Thallus with purple, ventral scales which seldom extend beyond the margin 2. REBOULIA

1. *Grimaldia* Raddi¹

Grimaldia fragrans (Balb.) Corda. On thin soil over limestone. Rare. Rutherford County.

Another species of *Grimaldia* has been recently collected in Davidson County by Dr. H. C. Bold of Vanderbilt University. Although it could not be identified with certainty it is probably *G. rupestris* (Nees) Lindenb.

2. *Reboulia* Raddi

Reboulia hemisphaerica (L.) Raddi. On moist banks and in crevices of rocks. Common. Anderson, Blount, *Grainger, Knox, Putnam, Roane, Rutherford, and Sevier Counties.

3. *Asterella* Beauv.

Asterella tenella (L.) Beauv. On moist open soil. Not common. Blount, Davidson, Grainger, Union and *Washington Counties.

III. MARCHANTIACEAE

KEY TO GENERA

1. Thallus lacking pores in the upper surface 2. DUMORTIERA
1. Thallus with pores 2

¹ Since the manuscript was completed *Grimaldia californica* Gottsche has been found in Polk Co.

2. Thallus lacking gemmae; pore surrounded by a single layer of cells; female receptacle terminated by a conical head 1. *CONOCEPHALUM*
 2. Thallus often with gemmae; pore surrounded by several tiers of cells; female receptacle terminated by spoke-like processes 3. *MARCHANTIA*

1. *Conocephalum* Wigg.

Conocephalum conicum (L.) Dum. On moist or wet rocks. Common. Anderson, Blount, *Hamilton, Knox, *Marion and Sevier Counties.

2. *Dumortiera* R. Bl. & Nees

Dumortiera hirsuta (Sw.) Nees. On wet rocks. Common. Blount, Davidson, Franklin, Hamilton, Knox, *Loudon, *Marion, Polk, Putnam, Rutherford, Sevier, Union and Van Buren Counties.

3. *Marchantia* L.

KEY TO SPECIES

1. Thallus seldom more than 6 mm. wide, growing on clay banks near dolomite 1. *domingensis*
 1. Thallus usually more than 12 mm. wide, growing in moist, burned-over areas or in springs below such areas 2. *polymorpha*

1. *Marchantia domingensis* Lehm. & Lindenb. On clay creek banks overlying dolomitic rocks. Not common. Anderson, Campbell, Knox and Union Counties. This species was reported from McMinn County by Evans (1910a). *Marchantia domingensis* is widely distributed in the tropics.

2. *Marchantia polymorpha* L. On moist soil following fires or in springs below such areas. Not common. Blount, Davidson, Johnson, *Knox, Marion and *Sevier Counties. This hepatic has been found covering several acres following a fire in the Shady Valley bog in Johnson County. For account of such invasions see Skutch (1929), Torrey (1932a, 1932b) and Graff (1935, 1936).

Order II. SPHAEROCARPALES

Only one family, *Sphaerocarpaceae*, and one genus, *Sphaerocarpos*, in Tennessee.

Sphaerocarpos Ludwig

Sphaerocarpos texanus Aust. On soil in a cultivated field. Rare. Knox County. The Tennessee plants exhibit many characters in common with *S. Michellii* Bellardi, but more in common with *S. texanus*.

Order III. METZGERIALES

KEY TO FAMILIES

1. Gametophyte always thalloid; sex organs borne on short, lateral, or reduced ventral branches, or if borne dorsally, not sunken I. METZGERIACEAE
 1. Gametophyte thalloid or leafy; if thalloid, the sex organs sunken in dorsal pockets II. PELLICEAE

I. METZGERIACEAE

KEY TO GENERA

1. Thallus with a distinct midrib 2
 1. Thallus without a distinct midrib 3. *RICCARDIA*
 2. Thallus less than 3 mm. wide, dichotomously branched; margin often with hairs 1. *METZGERIA*
 2. Thallus usually more than 6 mm. wide, simple or once forked; margin without hairs 2. *PALLAVICINIA*

1. *Metzgeria* Raddi

KEY TO SPECIES

1. Thallus with long, curved, marginal hairs; midrib only 2 cells wide on the underside 4. *hamata*
 1. Thallus with marginal hairs not consistently curved; midrib usually more than

- 2 cells wide on the underside 2
 2. Hairs borne only on margins and midrib of thallus 3
 2. Hairs borne on under-surface of wings of thallus as well as of margins and midrib 4
 3. Gemmae abundant, longer than wide, seldom with evident midrib, frequently giving rise to secondary gemmae before becoming detached..... 5. *myriopoda*
 3. Gemmae never present..... 1. *conjugata*
 4. Wing with an abundance of hairs; gemmae borne on the upper surface of the wings 2. *crassipilis*
 4. Wing with few scattered hairs; gemmae borne on the margins..... 3. *furcata*
1. *Metzgeria conjugata* Lindb. On moist shaded rocks. Not common. Grainger, Hamilton, Morgan, Sevier, and Van Buren Counties.
 2. *Metzgeria crassipilis* (Lindb.) Evans. On moist rocks and bark of trees. Not common. *Blount, Carter, *Cooke, *Grainger, Johnson and Sevier Counties.
 3. *Metzgeria furcata* (L.) Dum. On trees and rocks. Not common. Morgan and Sevier Counties.
 4. *Metzgeria hamata* Lindb. On moist rocks in the mountains. Rare. Sevier County. This species occurs in the tropics.
 5. *Metzgeria myriopoda* Lindb. On trees and rocks. Not common. Blount, Hamilton, Johnson, Knox, Marion and *Polk Counties. Also found in the tropics.

2. *Pallavicinia* S. F. Gray

Pallavicinia Lyellii (Hook.) Gray. On wet, sandy rocks and soils. Not rare. Fentress, Monroe, Morgan, *Sevier and Van Buren Counties.

3. *Riccardia* S. F. Gray

1. Thallus 2 or more mm. in width, thick and brittle..... 5. *pinguis*
 1. Thallus .5 to 2 mm. in width, not noticeably thick and brittle 2
 2. Thallus crescent-shaped in cross-section, with few branches..... 1. *incurvata*
 2. Thallus lens-shaped in cross-section, usually with many branches 3
 3. Thallus densely branched; branches with thin, transparent margins near the tip 3. *multifida*
 3. Thallus not densely branched; branches without thin transparent margins 4
 4. Thallus with irregular branching; branches broad and blunt..... 2. *latifrons*
 4. Thallus frequently with palmate branching; branches more attenuate 4. *palmata*
1. *Riccardia incurvata* Lindb. On moist clay bank. Rare. Knox County. This is the only locality in North America from which this liverwort has been reported.
 2. *Riccardia latifrons* Lindb. On moist soil and decaying wood. Uncommon. Campbell, Knox, Morgan and *Sevier Counties.
 3. *Riccardia multifida* (L.) S. F. Gray. On wet rocks and soil. Not common. Blount, Campbell, Johnson and Sevier Counties.
 4. *Riccardia palmata* (Hedw.) Carruth. On moist decaying wood. Rare. Sevier County.
 5. *Riccardia pinguis* (L.) S. F. Gray. In wet, shaded habitats. Rare. Sevier County. Andrews (1921) reported this species from Carter County.

II. PELLICEAE

KEY TO GENERA

1. Gametophyte thalloid, 6 to 15 mm. broad with wavy margins 2. PELLIA
 1. Gametophyte leafy, less than 4 mm. broad 1. FOSSOMBRONIA

1. *Fossombronia* Raddi

KEY TO SPECIES

1. Elaters short, with blunt ends, and annular as well as spiral thickenings..... 2. *cristula*
 1. Elaters longer, more tapering, with spiral thickenings only 2

2. Sculpturing on the spores often in the form of parallel ridges commonly not united at their ends.....4. *Wondraczeki*
2. Ridges on the spores joined at their ends, thus enclosing depressed areas..... 3
3. Ridges on spores high, enclosing depressed areas 10-13 microns in diameter.....1. *brasilensis*
3. Ridges on spores low, enclosing depressed areas 7-9 microns in diameter.....3. *foveolata*

1. *Fossombronia brasiliensis* Steph. On soil. Rare. Davidson Co. This species was reported from western Tennessee by Evans (1914b) as *F. salina*.

2. *Fossombronia cristula* Aust. On moist alluvial soils. Uncommon. Johnson and Sevier Counties.

3. *Fossombronia foveolata* Lindb. Moist open soil. Uncommon. Claiborne and Fentress Counties.

4. *Fossombronia Wondraczeki* (Corda) Dum. Soil of moist crevices. Rare. *Sevier County.

2. *Pellia* Raddi

Pellia epiphylla (L.) Corda. On wet rocks and sandy banks. Common in the mountains. *Blount, Campbell, Carter, Hamilton, Morgan and Sevier Counties.

Order IV. JUNGERMANNIALES

KEY TO FAMILIES

1. Leaf, if lobed, not complicate-bilobed 2
1. Leaf complicate-bilobed 5
2. Gametophyte extremely small, less than 1 mm. in width; leaf cleft to the middle, usually transversely inserted on the stemII. CEPHALOZIELLACEAE
2. Gametophyte varying in size, usually over 1 mm. in width; leaf entire, dentate, or lobed, obliquely or transversely inserted on the stem 3
3. Leaf deeply cut into ciliate or hair-like segments, or, if bifid, cleft two-thirds to three-fourths the depth of the leaf into two curved, long, slender, attenuate lobesIV. PTILIDIACEAE
3. Leaf not deeply cut into filiform segments; if bifid, not so deeply cleft, with shorter lobes 4
4. Leaf succubous or transversely inserted; perianth laterally compressed, or cylindrical, or ovate, and plicate or trigonous with the third angle always dorsal; male bracts each with one or two antheridia.....I. LOPHOZIEACEAE
4. Leaves usually incubous, sometimes transversely inserted, rarely succubous; perianth trigonous with the third angle always ventral; male bracts each with one to ten antheridiaIII. CEPHALOZIEACEAE
5. Dorsal lobe of the leaf smaller than the ventralV. SCAPANIACEAE
5. Ventral lobe smaller than the dorsal 6
6. Underleaves never present; rhizoids arising from protuberances on the ventral lobe of leafVI. RADULACEAE
6. Underleaves usually present (except in *Cololejeunea*); rhizoids when present, arising from the ventral surface of the base of the underleaf 7
7. Gametophyte small, usually less than 1 mm. wide; elaters attached by one end to the capsule wallVIII. LEJEUNEACEAE
7. Gametophyte large, about 2 or more mm. wide; elaters short, free.....VII. PORELLACEAE

I. LOPHOZIEACEAE

KEY TO GENERA

1. Leaf often with marginal rhizoids9. *ACROBOLBUS*
1. Leaf without marginal rhizoids 2
2. Leaf lobed or toothed 7
2. Leaf not lobed and entire 3
3. Underleaf with two long slender lobesI. *CHILOSCYPHUS*
3. Underleaves absent, or if present, minute, not lobed 4
4. Gametophyte minute, not easily seen without a lens; growing on bark of fir11. *MYLIA*

4. Gametophyte larger, easily seen without a lens; growing on soil, rocks or decaying wood 5
5. Walls of leaf-cells noticeably thickened at their intersections; underleaves absent 5. JUNGERMANNIA
5. Walls of leaf-cells not noticeably thickened at their intersections, or, if thickened, underleaves present 6
6. Gametophyte large, often with a reddish-brown tinge; leaf-cells lacking oil bodies 4. JAMESONIELLA
6. Gametophyte small or, if large, leaf-cells usually with oil bodies 12. NARDIA
7. Underleaves present 8
7. Underleaves absent or few and inconspicuous 10
8. Underleaf not bifid, its margins sometimes toothed 3. HARPANTHUS
8. Underleaf bifid, its margins sometimes toothed 9
9. Underleaf with short lateral teeth near the base 6. LOPHOCOLEA
9. Underleaf without short lateral teeth near the base 2. GEOCALYX
10. Leaves inserted on stems obliquely 11
10. Leaves inserted on stems transversely 13
11. Leaf bilobed or trilobed and often toothed 12
11. Leaf often toothed but not deeply lobed 13. PLAGIOCHILA
12. Plants less than 5 mm. wide; leaf bilobed; lobe ovate and obtuse 7. GYMNOCOLEA
12. Plants usually more than 1 mm. wide; leaf bilobed or trilobed 8. LOPHOZIA
13. Leaf bilobed, lobes equal; gametophyte growing on wet rocks or cliffs 10. MARSUPELLA
13. Leaf bilobed, lobes unequal, or, if equal, gametophyte growing on decaying wood or soil 14. SPHENOBUS

1. *Chiloscyphus* Corda

KEY TO SPECIES

1. Leaf-cells 21-28 microns in diameter; gametophyte dark green, growing submerged 3. *rivularis*
1. Leaf-cells more than 28 microns in diameter; gametophyte paler green, not submerged 2
2. Gametophyte pale green or pale yellowish-green; leaf-cells very transparent 1. *pallascens*
2. Gametophyte yellow, dull or brownish-green; leaf-cells only slightly transparent 2. *polyanthus*

1. *Chiloscyphus pallascens* (Ehrh.) Dum. On moist soil or decaying logs. Rare. *Knox, and *Sevier Counties. Probably these records should be added to those for *C. polyanthus* var. *fragilis*, from which this species is doubtfully distinct.

2. *Chiloscyphus polyanthus* (L.) Corda. Moist soil. Rare. *Blount and Morgan Counties. Andrews (1921) reported this hepatic from Carter County.

The var. *fragilis* (Roth) C. Muell. is distinguished from the species by larger leaf-cells which are 30-45 microns in diameter as compared to 28-33 microns for *C. polyanthus*. It has been collected in wet places in Carter County.

3. *Chiloscyphus rivularis* (Schr.) Loeske. Submerged in brooks. Rare. Carter and Sevier Counties. In spite of its distinct appearance there is some question whether or not this hepatic is more than a variety of *C. polyanthus*.

2. *Geocalyx* Nees

Geocalyx graveolens (Schr.) Nees. On moist rocks and cliffs. Not common. *Blount, and Sevier Counties. This species usually exhibits a yellowish-green color unlike other hepatics.

3. *Harpanthus* Nees

Harpanthus scutatus (W. & M.) Spruce. In moist places. Rare. Sevier County.

4. *Jamesoniella* (Spruce) Schiffn.

Jamesoniella autumnalis (DC) Steph. On moist rocks and decaying wood. Common. *Blount, Johnson, Knox, Sevier and Washington Counties.

5. *Jungermannia* L.

Jungermannia lanceolata Schrad. On moist soil. Rare. *Blount County.

6. *Lophocolea* Dum.

KEY TO SPECIES

1. Mature leaves near stem-apex entire or emarginate.....4. *heterophylla*
1. Mature leaves near stem-apex never entire 2
2. Leaf-cells 28-35 microns in diameter; gametophyte dioicous; rarely with perianths2. *bidentata*
2. Leaf-cells 33-50 microns in diameter; gametophyte monoicous; frequently with perianths 3
3. Leaf-cells 40-50 microns in diameter; gametophyte dark green.....1. *alata*
3. Leaf-cells 33-42 microns in diameter; gametophyte yellowish-green.....3. *cuspidata*
1. *Lophocolea alata* Mitt. ex Larter. Moist rocks. Rare. Sevier County.
2. *Lophocolea bidentata* (L.) Dum. Moist soil and rocks. Uncommon. Blount and Sevier Counties.
3. *Lophocolea cuspidata* Limpr. On moist limestone rock. Rare. Rutherford County.
4. *Lophocolea heterophylla* (Schrad.) Dum. On moist rocks and decaying wood. Common. Blount, Davidson, *Grainger, Hamilton, Hamilton, Knox, Sevier and Union Counties. Andrews (1921) reported this species from Carter County.

7. *Gymnocolea* Dum.

Gymnocolea inflata (Huds.) Dum. (*Lophozia inflata* Huds.). Moist crevices of cliff. Known only from Alum Cave, Sevier County. This has not been reported previously south of New England.

8. *Lophozia* Dum.

KEY TO SPECIES

1. Stem with slender, small-leaved apex; leaf usually trilobed.....1. *attenuata*
1. Stem-apex not so differentiated; leaf usually bilobed 2
2. Stem translucent; gemmae not known2. *badensis*
2. Stem opaque; gemmae often present..... 3
3. Stem thick; upper leaves conspicuously toothed; dioicous.....5. *incisa*
3. Stem slender; upper leaves not so conspicuously toothed; paroicous 4
4. Stem seldom longer than 6 mm.; walls of leaf-cells strongly thickened.....3. *bicrenata*
4. Stem averaging 10 mm. in length; walls of leaf-cells thin.....4. *excisa*
1. *Lophozia attenuata* (Mont.) Dum. On moist peaty soil on mountain tops. Rare. Sevier County.
2. *Lophozia badensis* (Gottsche) Schiffn. In moist crevices of bluffs. Rare. Roane County.
3. *Lophozia bicrenata* (Schmid.) Dum. On clay banks and soils. Common. Blount, Knox, Sevier and Union Counties. Andrews (1921) reported this species from Carter County.
4. *Lophozia excisa* (Dicks.) Dum. Moist habitats in the high mountains. Rare. Sevier County.
5. *Lophozia incisa* (Schrad.) Dum. On moist peaty soil in the high mountains. Rare. Sevier County.

9. *Acrobolbus* Nees

Acrobolbus rhizophyllus Sharp. On wet ledges and rocks above 4,000 feet. Rare. Sevier County. The rhizoids on the leaf-margins and the peculiar pale blue-green color make this hepatic very easy to recognize. The remaining species of the genus in the western hemisphere are found in South America.

10. *Marsupella* Dum.

KEY TO SPECIES

1. Leaf bilobed to a depth of not more than one-fifth of its length; margin recurved1. *emarginata*

1. Leaf bilobed to a depth exceeding one-fourth of its length; margin usually plane..... 2
2. Gametophyte growing in water, flaccid; lower leaves green..... 2. *sphacelata*
2. Gametophyte not definitely aquatic, not flaccid; leaves brown..... 3. *Sullivantii*

1. *Marsupella emarginata* (Ehrh.) Dum. On moist cliffs and rocks. Rare. Sevier County.

2. *Marsupella sphacelata* (Gies.) Lindb. On boulders in brooks. Rare. Sevier County.

3. *Marsupella Sullivantii* (De Not.) Evans. On moist cliffs and rocks. Uncommon. *Blount and Sevier Counties. This species is very closely related to *M. sphacelata*.

11. *Mylia* (S. F. Gray) Lindb.

Mylia cuneifolia (Hook.) S. F. Gray. On bark of living *Abies Fraseri* (Pursh) Poir. on the summits of our highest mountains. Uncommon. Sevier County.

12. *Nardia* S. F. Gray emend. Lindb.

KEY TO SPECIES

1. Leaf with border of larger cells..... 2
1. Leaf without differentiated border..... 3
2. Central leaf-cells averaging about 25 microns in diameter; trigones none or minute..... 1. *crenulata*
2. Central leaf-cells averaging about 35 microns in diameter; trigones distinct..... 2. *crenuliformis*
3. Stem slender; leaf-cells without oil bodies..... 3. *hyalina*
3. Stem thick; leaf-cells usually with persistent oil bodies..... 4. *scalaris*

1. *Nardia crenulata* (Sm.) Dum. Moist, sandy, clay banks. Common in the mountains. Blount, *Carter, Johnson, Knox and Sevier Counties.

2. *Nardia crenuliformis* (Aust.) Lindb. Moist rock. Rare. *Sevier County.

3. *Nardia hyalina* (Lyll) Carr. Moist soil. Rare. *Blount County.

4. *Nardia scalaris* (Schrad.) Corda. Moist peaty soil on summit of Mt. LeConte. Rare. Sevier County. This hepatic is much more frequent northward.

13. *Plagiochila* Dum.

KEY TO SPECIES

1. Gametophyte less than 1 cm. in length, with caducous leaves, growing only on the bark of living fir, birch or spruce..... 5. *tridenticulata*
1. Gametophyte larger; leaves not noticeably caducous; growing on substrata other than fir or spruce..... 2
2. Posterior basal margin of leaves seldom reflexed..... 3
2. Posterior basal margin of leaves conspicuously reflexed..... 5
3. Margin of leaf entire or, if denticulate, with more than 10 small teeth..... 1. *asplenioides*
3. Margin of leaf dentate with 10 or less teeth..... 4
4. Leaf rectangular-ovate, not noticeably narrowed at the base..... 2. *Austini*
4. Leaf obovate, distinctly narrowed at the base..... 4. *Sullivantii*
5. Posterior margins of leaves plane and dentate beyond the reflexed base..... 3. *ludoviciana*
5. Posterior margins of leaves repand-undulate beyond the reflexed base..... 6. *undata*

Descriptions of the following species are found in the writings of Evans (1896, 1914a).

1. *Plagiochila asplenioides* (L.) Dum. On moist rocks, soil and bases of trees. Rather common. Blount, *Grainger, Marion, Rutherford and Sevier Counties.

2. *Plagiochila Austini* Evans. On moist rocks. Not common. Blount and Sevier Counties.

3. *Plagiochila ludoviciana* Sull. On moist rocks. Not common. Blount, Greene and Marion Counties.

4. *Plagiochila Sullivantii* Gottsche. On moist rocks. Not common. Blount, *Cocke and Sevier Counties.

5. *Plagiochila tridenticulata* Tayl. On the bark of living trees about 6,000 feet in the mountains. Rare. *Carter and Sevier Counties.

6. *Plagiochila undata* Sull. On shaded rocks. Not common. Blount and *Polk Counties. Evans (1896) suggests that *P. crispata* Gottsche of Mexico, is probably identical with this species.

There is an apparently undescribed species of *Plagiochila* in the Great Smoky Mountains and neighboring highlands, which has caducous, filiform teeth on the leaves. It will be described by Dr. H. L. Blomquist of Duke University.

14. *Sphenolobus* (Lindb.) Steph.

KEY TO SPECIES

1. Leaf with 3 unequal lobes.....1. *exsectus*
1. Leaf with 2 almost equal lobes.....2. *Michauxii*

1. *Sphenolobus exsectus* (Schmid.) Steph. On bases of trees and peaty soils at high elevations. Not common. Carter and Sevier Counties.

2. *Sphenolobus Michauxii* (Web.) Steph. On decaying logs and bases of trees in the fir forests at high elevations. Rare. Sevier County.

II. CEPHALOZIACEAE

Cephaloziella (Spruce) Schiffn.

KEY TO SPECIES

1. Stem and leaves not spinose-papillose.....1. *byssacea*
1. Stem and leaves very spinose-papillose.....2. *spiniaculis*

1. *Cephaloziella byssacea* (Roth) Warnst. On moist soil and rocks. Rare. *Grainger and *Knox Counties.

2. *Cephaloziella spiniaculis* Douin. On moist boulders. Very rare. Sevier County.

III. CEPHALOZIACEAE

KEY TO GENERA

1. Underleaves lacking or very minute except near the sex organs.....2
1. Underleaves rather conspicuous.....3
2. Leaf deeply bilobed.....3. *CEPHALOZIA*
2. Leaf not lobed.....5. *ODONTOSCHISMA*
3. Leaf entire or denticulate, not deeply cleft.....4
3. Leaf deeply cleft into 3 or more lobes.....4. *LEPIDOZIA*
4. Trigones of cell-walls present and rather well defined.....1. *BAZZANIA*
4. Trigones of cell-walls lacking or rather minute.....2. *CALYPOGEIA*

1. *Bazzania* S. F. Gray

KEY TO SPECIES

1. Stem with some caducous leaves.....2
1. Stem without caducous leaves.....3
2. Gametophyte light green; stem large, usually somewhat denuded; leaf-apex obtuse with 2 or 3 teeth.....1. *denudata*
2. Gametophyte reddish-brown or darker; stem filiform, usually extremely denuded; leaf-apex generally acute and entire.....2. *nudicaulis*
3. Leaf deflexed, especially when dry; apex obliquely truncate.....3. *tricrenata*
3. Leaf generally plane, even when dry; apex transversely truncate.....4. *trilobata*

Descriptions are found in the monograph by Fulford (1936).

1. *Bazzania denudata* (Torr.) Trevis. On bases of trees, rocks and occasionally logs at high elevations. Not common. Carter, *Cocke and Sevier Counties.

2. *Bazzania nudicaulis* Evans. On the bark of living *Abies Fraseri* (Pursh) Poir. above 5,000 feet. Rare. Carter and Sevier Counties. Endemic in the Southern Appalachians.

3. *Bazzania tricrenata* (Wahlenb.) Trevis. On rocks, soil, bases of trees at high elevations, also on logs. Not common. Sevier County.

4. *Bazzania trilobata* (L.) S. F. Gray. On soil, rocks, bases of trees and logs. Common. *Blount, *Cocke, *Grainger, Hamilton, Morgan and Sevier Counties. This is the only species of *Bazzania* which has been found at lower elevations in Tennessee.

2. *Calypogeia* Raddi

KEY TO SPECIES

1. Underleaf large, rounded or, if bilobed, lobes broad and round, sinus shallow 4. *Trichomanis*
1. Underleaf small, bilobed to a depth of one-fourth or more; lobes seldom rounded 2
2. Underleaf strongly bilobed, with subulate segments; free walls of leaf-cells verruculose 1. *arguta*
2. Underleaf bilobed, but without subulate segments; free walls of leaf-cells smooth 3
3. Underleaf twice as wide as long 2. *fissa*
3. Underleaf less than twice as wide as long 3. *succica*

1. *Calypogeia arguta* Nees & Mont. (C. *Sullivantii* Aust.) On very moist banks. Not common. *Blount, *Grainger and *Morgan Counties. The writer does not believe that *C. Sullivantii* merits specific rank.

2. *Calypogeia fissca* (L.) Raddi. On moist soil. Not common. Grainger, *Monroe and Sevier Counties.

3. *Calypogeia suecica* (Arn. & Perss.) C. Muell. On logs and moist soil. Rare. Sevier County.

4. *Calypogeia Trichomanis* (L.) Corda. On very moist soil. Common. Blount, Johnson, *Morgan, Rutherford, Sevier and Union Counties.

3. *Cephalozia* Dum.

KEY TO SPECIES

1. Leaf very deeply concave like a full-bellied sail, with 2 filiform points..... 5. *curvifolia*
1. Leaf not deeply concave, nor with filiform points 2
2. Stem with flagellate branches 3
2. Stem without flagellate branches 4
3. Apices of leaf-lobes frequently obtuse; cells 20-30 microns in diameter..... 1. *ambigua*
3. Apices of leaf-lobes sharply acute; cells 30-50 microns in diameter..... 2. *bicuspidata*
4. Gametophyte relatively dark-colored; leaf-cells small, 16-21 microns in diameter, thick-walled; leaf-lobes seldom connivent..... 3. *catenulata*
4. Gametophyte green; leaf-cells larger than 21 microns in diameter, thin walled; leaf-lobes usually connivent 5
5. Leaf-cells 40-60 microns in diameter; leaf-sinus almost circular..... 4. *connivens*
5. Leaf-cells 23-35 microns in diameter; leaf-sinus semi-circular..... 6. *media*

1. *Cephalozia ambigua* Massal. On moist soil on mountain summits. Rare. Sevier County.

2. *Cephalozia bicuspidata* (L.) Dum. On moist soil. Not common. *Blount, Johnson, *Morgan and Sevier Counties.

3. *Cephalozia catenulata* (Hueben.) Spruce. On logs and moist rocks. Not common. Blount, Carter, *Polk and Sevier Counties.

4. *Cephalozia connivens* (Dicks.) Lindb. On moist peaty soil and logs. Rare. Sevier County.

5. *Cephalozia curvifolia* (Dicks.) Dum. On logs. Common. Blount, *Cocke, *Grainger, Knox, Morgan and Sevier Counties. Some bryologists place this species in Mitten's genus *Nowellia*.

6. *Cephalozia media* Lindb. On moist soil and logs. Common in the mountains. Blount, Campbell, Cumberland, *Morgan, Roane and Sevier Counties.

4. *Lepidozia* Dum.

KEY TO SPECIES

1. Leaf large, cleft less than one-half the way to its base into three or four broad segments 1. *reptans*
1. Leaf small, cleft nearly to its base into three slender segments..... 2. *sylytica*

1. *Lepidozia reptans* (L.) Dum. On moist soil, logs and rocks at high elevations. Not common. *Blount and Sevier Counties.

2. *Lepidozia sylvatica* Evans. On moist soil in the mountains. Not common. Blount, *Morgan and Sevier Counties.

5. *Odontoschisma* Dum.

KEY TO SPECIES

1. Leaves near the apex of the stem often differing in size (smaller) and shape from the others.....1. *denudatum*
1. Leaves at the apex of the stem not essentially different from the others 2. *prostratum*
 1. *Odontoschisma denudatum* (Mart.) Dum. On logs and moist soil. Uncommon. *Blount, Campbell, *Fentress, Morgan and Sevier Counties.
 2. *Odontoschisma prostratum* (Sw.) Trevis. On moist soil. Uncommon. Blount, Campbell, *Grainger, Lincoln, *Morgan, *Polk and Sevier Counties.

IV. PTILIDIACEAE

Key to genera

1. Leaf deeply cleft into two long, linear-lanceolate, often curved lobes...3. *HERBERTA*
1. Leaf entirely or ultimately divided into three—many filiform segments.....2
 2. Leaf completely divided into 3 or 4 filiform segments only one cell in width.....1. *BLEPHAROSTOMA*
 2. Leaf divided distally into many filiform segments; leaf-base undivided.....3
3. Gametophyte green or brown; leaf-cells of lamina not very elongated; trigones large; free walls of leaf-cells smooth.....2. *PTILIDIUM*
3. Gametophyte whitish-green; leaf-cells of lamina much longer than wide; trigones none; free walls of leaf-cells striate-punctate.....4. *TRICHOCOLEA*

1. *Blepharostoma* Dum.

Blepharostoma trichophyllum (L.) Dum. On bases of trees, on logs and moist soil at high elevations. Rare. *Blount, Carter and Sevier Counties.

2. *Ptilidium* Nees

Ptilidium pulcherrimum (Web.) Hamp. On logs. Rare. Campbell County. Evidently the southernmost known station for this species.

3. *Herberta* S. F. Gray

Herberta tenuis Evans. On trees and rocks in the mountains. Not common except at high altitudes. Blount, Carter, *Cocke and Sevier Counties.

4. *Trichocolea* Dum.

Trichocolea tomentella (Ehrh.) Dum. On wet rocks and soil. Common. Blount, Knox, Morgan, Polk, Putnam and Sevier Counties.

V. SCAPANACEAE

KEY TO GENERA

1. Ventral lobe of leaf curved, oblong-lanceolate.....1. *DIPLOPHYLLUM*
1. Ventral lobe of leaf rounded-ovate.....2. *SCAPANIA*

1. *Diplophyllum* Dum.

KEY TO SPECIES

1. Leaf entire, apex rounded.....1. *Andrewsii*
1. Leaf denticulate, apex acute.....2. *apiculatum*
 1. *Diplophyllum Andrewsii* Evans. On moist, sandy, clay banks in the mountains. Rare. *Carter, and *Sevier Counties.
 2. *Diplophyllum apiculatum* (Evans) Steph. On moist soil and rocks. Common. *Anderson, Blount, Carter, *Grainger, Knox, Morgan and Sevier Counties.

2. *Scapania* Dum.

KEY TO SPECIES

1. Leaf denticulate; gemmae one-celled 1. *nemorosa*
 1. Leaf entire; gemmae mostly two-celled 2. *undulata*
 1. *Scapania nemorosa* (L.) Dum. On moist soil and rocks. Common. *Blount, Carter, Cheatham, Cumberland, Hamilton, Knox, Marion, Monroe, *Morgan, *Polk, and Sevier Counties
 2. *Scapania undulata* (L.) Dum. On rocks in water. Not common. *Blount, *Grainger and Sevier Counties.

VI. RADULACEAE

Radula Dum.

KEY TO SPECIES

1. Leaf often with gemmae; rhizoids always present 2
 1. Leaf never with gemmae; rhizoids sometimes lacking 4
 2. Ventral lobe broadly rounded, extending across and beyond the stem 1. *andicola*
 2. Ventral lobe bluntly pointed, rarely extending over half-way across the stem 3
 3. Gametophyte dioicous, rarely with sex organs, especially when gemmae are abundant 2. *caloosicensis*
 3. Gametophyte paroicous, sex organs usually present even when gemmae are abundant 3. *complanata*
 4. Leaf without caducous dorsal lobes 6. *tenax*
 4. Leaf with caducous dorsal lobes 5
 5. Leaf falcate; the ventral lobe fused to the stem for nearly its entire length 5. *Sullivantii*
 5. Leaf only slightly falcate; the ventral lobe free for at least half its length 4. *obconica*
 Descriptions are found in Castle's monograph (1925).
 1. *Radula andicola* Steph. On moist bluffs and rocks. Common. Blount, Campbell, Knox, Marion, Sevier and Union Counties.
 2. *Radula caloosicensis* Aust. On the bark of trees. Rare. *Fentress, Johnson and Sevier Counties.
 3. *Radula complanata* (L.) Dum. On moist rocks and tree trunks. Uncommon. *Anderson, *Knox, Marion and *Sevier Counties.
 4. *Radula obconica* Sull. On moist rocks and tree trunks. Uncommon. Blount, Campbell, Hamilton, Marion, Sevier and Union Counties.
 5. *Radula Sullivantii* Aust. On moist rocks in the mountains. Not common. Blount, Campbell, Johnson, Morgan and Sevier Counties.
 6. *Radula tenax* Lindb. On moist rocks; occasionally on trees and logs in the mountains. Not common. Campbell, *Cocke and Sevier Counties.

VII. PORELLACEAE

Porella (Dill.) Lindb. (*Madotheca* Dum.)

KEY TO SPECIES

1. Underleaf considerably wider than the stem 1. *platyphylloidea*
 1. Underleaf slightly wider than the stem 2
 2. Leaves and underleaves entire; plants aquatic for at least part of the year 2. *pinnata*
 2. Leaf often repand-dentate; underleaf frequently bifid or uncleft and denticulate; plants never aquatic 3. *wataugensis*
 1. *Porella platyphylloidea* (Schwein.) Lindb. [*Madotheca platyphylloidea* (Schwein.) Dum.] On rocks and trees. Common. *Anderson, Blount, Carter, Grainger, *Hamilton, Knox, *Lincoln, Morgan, Rutherford, Scott, Sevier, *Unicoi, Washington and Wilson Counties. *Porella platyphylla* (L.) Lindb. reported by Haynes (1916) from Tennessee is probably this species.
 2. *Porella pinnata* L. [*Madotheca Porella* (Dicks.) Nees] On stones and logs which are at times submerged. Common. Anderson, Blount, Cheatham, Hamilton, Knox, Marion, Rutherford, Sevier, Unicoi and Van Buren Counties.
 3. *Porella wataugensis* (Sull.) Underw. (*Madotheca wataugensis* Sull.) On moist,

shaded rocks in the mountains. Rare. Blount County. This species is probably a variety of *Porella Cordeana* (Hueben.) Evans (*Porella dentata* Lindb.).

VIII. LEJEUNEACEAE *

KEY TO GENERA

1. Ventral lobe developed as hollow, helmet-shaped or cylindrical sac 2
1. Ventral lobe variously shaped but never in the form of a sac 3
 2. Ventral lobe attached to stem as well as to the dorsal lobe, the latter seldom pointed 1. FRULLANIA
 2. Ventral lobe attached to the dorsal lobe but not to the stem; dorsal lobe pointed 2. JUBULA
3. Underleaves absent 3. COLOLEJEUNEA
4. Underleaves present 4
 4. Underleaf entire 8. LEUCOLEJEUNEA
 4. Underleaf bifid 5
5. Dorsal lobe subacute, acute or acuminate at the apex 6
5. Dorsal lobe obtuse or rounded at the apex 8
 6. Dorsal lobe long-acuminate; underleaf with spreading, subulate lobes 5. DREPANOLEJEUNEA
 6. Dorsal lobe not long-acuminate; underleaf without subulate lobes 7
7. Underleaf with rounded lobes and a broad shallow sinus 6. HARPALEJEUNEA
7. Underleaf with acuminate lobes, often obtusely dentate, with a sinus one-fourth to one-half its length 4. CROSSOTOLEJEUNEA
8. Dorsal lobe suberect or obliquely spreading; underleaf with slender, often acuminate lobes 9. MICROLEJEUNEA
8. Dorsal lobe widely spreading; lobes of the underleaf neither acuminate or very slender 9
9. Dorsal lobe often caducous; posterior margin of dorsal lobe with little or no indentation at the junction of the ventral lobe; gametophyte often with microphyllous branches 10. RECTOLEJEUNEA
9. Dorsal lobe never caducous; posterior margin of dorsal lobe with a distinct indentation at the junction with the ventral lobe; branches of gametophyte never microphyllous 7. LEJEUNEA

1. *Frullania* Raddi

1. Leaf with a median line of discolored cells; ventral lobe longer than broad 1. *Asagrayana*
1. Leaf without a line of discolored cells; ventral lobe as broad as long 2
 2. Underleaf plainly cordate at the base 4. *plana*
 2. Underleaf not cordate at the base 3
3. Leaves very squarrose when moist 7. *squarrosa*
3. Leaves little if at all squarrose when moist 4
 4. Ventral lobule usually explanate, not inflated 5. *riparia*
 4. Ventral lobule usually inflated, seldom explanate 5
5. Underleaf frequently dentate or crenate; ventral lobe inflated above, compressed at base 2. *Brittoniae*
5. Underleaf entire; ventral lobe inflated throughout 6
 6. Perianth smooth 3. *eboracensis*
 6. Perianth with roughened ridges 6. *saxicola*

Descriptions are found in the monograph by Evans (1897).

1. *Frullania Asagrayana* Mont. On the bark of trees and rocks. Common, particularly in the mountains. Anderson, Blount, *Cocke, *Grainger, Johnson and Sevier Counties.

2. *Frullania Brittoniae* Evans. On bark of trees and rocks. Not common. Carter, Johnson and Sevier Counties.

* The preparation of the keys for this family was facilitated by the work of Morrison (1938).

3. *Frullania eboraensis* Gottsche. On bark of trees. Not common. *Sevier County.
 4. *Frullania plana* Sull. On rocks in the mountains. Uncommon. Sevier County.
 5. *Frullania riparia* Hampe. On bark of trees. Common. *Blount, Cheatham, Knox, *Polk, Rutherford, *Scott and Washington Counties.
 6. *Frullania saxicola* Aust. On rocks. Rare. *Washington County.
 7. *Frullania squarrosa* (R. Bl. & Nees) Dum. On bark of trees and rocks. Common. *Anderson, *Blount, *Cocke, *Fentress, Knox, Sevier and Washington Counties.

2. *Jubula* Dum.

Jubula pennsylvanica (Steph.) Evans. On moist or wet rocks. Rather common in the mountains. Blount, Fentress, Morgan, Roane and Sevier Counties.

3. *Cololejeunea* (Spruce) Schiffn.

KEY TO SPECIES

1. Dorsal surface of the leaf-lobe tuberculate 2
 1. Dorsal surface of the leaf-lobe not tuberculate 3. *minutissima*
 2. Ventral surface of the lobule tuberculate 1. *ornata*
 2. Ventral surface of the lobule not tuberculate 2. *Biddlecomiae*

For descriptions of these species see the work of Evans (1928).

1. *Cololejeunea ornata* Evans. Over mosses on dolomite. Anderson County. Savage's Garden at Coal Creek is the type locality and the only station known in the State.

2. *Cololejeunea Biddlecomiae* (Aust.) Evans. On bark or rocks. Not common. Knox, Rutherford, Sevier and Washington Counties.

3. *Cololejeunea minutissima* (Sm.) Schiffn. On tree trunk. Rare. Anderson County.

4. *Crossotolejeunea* (Spruce) Schiffn.

Crossotolejeunea bermudiana Evans. On calcareous rocks. Rare. Marion County. Previously reported only from Bermuda and Florida.

5. *Drepanolejeunea* (Spruce) Schiffn.

Drepanolejeunea bidens (Steph.) Evans. On bark of trees. Rare. Blount County. Also found in the tropics, but not in the Coastal Plain.

6. *Harpalejeunea* (Spruce) Schiffn.

Harpalejeunea ovata (Hook.) Schiffn. On rocks and bark of trees. Not very common. Blount, Greene, Johnson and Sevier Counties.

7. *Lejeunea* Lib.

KEY TO SPECIES

1. Underleaf as large or larger than the ventral lobe 1. *cavifolia*
 1. Underleaf smaller than the ventral lobe 2
 2. Dorsal lobe and underleaves distinctly crenulate on the margins 2. *patens*
 2. Dorsal lobe and underleaves entire 3. *glaucescens*

1. *Lejeunea cavifolia* (Ehrh.) Lindb. On rocks. Uncommon. Hamilton, Rutherford and Sevier Counties.

2. *Lejeunea glaucescens* Gottsche. On rocks. Extremely rare. Rutherford County. The nearest known stations are in Florida.

3. *Lejeunea patens* Lindb. On rocks in the mountains. Not very common. Blount and Sevier Counties.

8. *Leucolejeunea* Evans

KEY TO SPECIES

1. Ventral lobe with an acute and often pointed apex, its free margin strongly involute 1. *unciloba*
 1. Ventral lobe with a blunt or rounded apex; the free margin not so strongly involute 2. *clypeata*

1. *Leucolejeunea unciloba* (Lindb.) Evans. Usually on trees, particularly beech.

Rather common. Anderson, Blount, Campbell, Hamilton, Knox and Morgan Counties.
 2. *Leucolejeunea clypeata* (Schw.) Evans. Usually on rocks. Rather common. Blount, Campbell, Cumberland, Greene, Marion and Sevier Counties.

9. *Microlejeunea* (Spruce) Jack & Steph.

KEY TO SPECIES

1. Underleaf longer than wide and divided for at least more than $\frac{1}{2}$ its length..... 2
1. Underleaf approximately as long as wide and divided for about $\frac{1}{2}$ its length..... 3
2. Ventral lobe variable in size from $\frac{1}{2}$ the length of the dorsal lobe to very minute; cell-walls thin 1. *laetevirens*
2. Ventral lobe consistently $\frac{1}{2}$ to $\frac{3}{4}$ the length of the dorsal lobe; cell-walls somewhat thickened 2. *ulicina*
3. Ventral lobe approximately $\frac{1}{2}$ the size of the dorsal lobe; median leaf-cells 18-20 microns in diameter 3. *Ruthii*
3. Ventral lobe nearly as large as the dorsal lobe; median leaf-cells 12-13 microns in diameter 4. *bullata*

1. *Microlejeunea laetevirens* (N. & W.) Evans. On siliceous rocks. Rather common. Campbell, Greene, Marion, Sevier and Unicoi Counties.

2. *Microlejeunea ulicina* (Tayl.) Evans. On trees. Rather rare. Blount, Cumberland, Johnson and Sevier Counties.

3. *Microlejeunea Ruthii* Evans. On trees. Rare. Sevier County. The type material was collected in Polk County by Mr. Albert Ruth and described by Evans (1902).

4. *Microlejeunea bullata* (Tayl.) Evans. On rocks. Not very common. Cheatham, Cumberland, Marion and Sevier Counties.

10. *Rectolejeunea* Evans

Rectolejeunea Maxonii Evans. On rocks and trees. Rare. Anderson and Cocke Counties.

Class II. SPHAGNEAE

Only one order, *Sphagnales*, one family, *Sphagnaceae*, and one genus, *Sphagnum*, in the class.

Sphagnum (Dill.) L.

KEY TO SPECIES*

1. Cortical cells of the stem and branches reinforced by spiral fibril-bands 2
1. Cortical cells of the stem and branches without fibril-bands 4
2. Chlorophylliferous cells of the branch-leaves usually entirely included, or occasionally about equally exposed on both surfaces 1. *magellanicum*
2. Chlorophylliferous cells of the branch-leaves usually triangular in section, with the base exposed on the inner surface of the leaf 3
3. Chlorophylliferous cells of the branch-leaves usually isosceles-triangular in section 2. *palustre*
3. Chlorophylliferous cells of the branch-leaves usually equilateral-triangular in section 3. *imbricatum*
4. Cortical cells of the branches uniform, each with a pore at the upper end 4. *compactum*
4. Cortical cells of the branches of two kinds, the larger, retort-cells with a neck and a pore, in the axils of the leaves; or if uniform, without pores 5
5. Stem-leaves with the membrane of the hyaline cells mostly resorbed on the outer surface, on the inner with membrane gaps only in the apical cells. 5. *squarrosum*
5. Stem-leaves with the membrane of the hyaline cells usually not greatly resorbed on the outer surface, or, if so, resorbed on both surfaces producing a very lacerate leaf apex 6

* This key is adapted from that in the excellent monograph "Sphagnales," by Andrews (1913).

6. Chlorophylliferous cells of the branch-leaves exposed exclusively or more fully on the outer surface; or, if with central lumen and approximately equal exposure, the pigment brown 7
6. Chlorophylliferous cells of the branch-leaves exposed exclusively or more fully on the inner surface; or, if with central lumen and approximately equal exposure, the pigment red 8
7. With many fascicled branches; chlorophylliferous cells of the branch-leaves exposed equally on both surfaces or more fully on the outer one..... 6. *subsecundum*
7. With few or no fascicled branches; chlorophylliferous cells of the branch-leaves usually exposed a little more fully on the inner surface..... 7. *Pylaeisii*
8. Stem-leaves lacerate across the broad, truncate apex 8. *Girgensohnii*
8. Stem-leaves not noticeably lacerate near the apex 9
9. Hyaline cells of the branch-leaves smaller, their free convexity on the outer surface mostly less than one half their diameter 10
9. Hyaline cells of the branch-leaves large in section, their free convexity on the outer surface usually more than one half their diameter 11
10. Stem-leaves large, lingulate to lingulate-ovate, one and one-half or more times as long as wide 9. *capillaceum*
10. Stem-leaves smaller, triangular to lingulate-triangular, mostly as wide as long 10. *quinquefarium*
11. Marg'n of the branch-leaves entire 11. *tenerum*
11. Margin of the branch-leaves denticulate 12. *tabulare*

1. *Sphagnum magellanicum* Brid. Edge of spring. Rare. Sevier County.

2. *Sphagnum palustre* L. Wet soil. Not common. Franklin, Marion, Polk, *Roane and Sevier Counties.

3. *Sphagnum imbricatum* Hornsch. Wet soils. Not common. Bledsoe, Fentress, Morgan, Polk, Roane and Sevier Counties.

The variety *affine* (R. & C.) Warnst., which differs in the complete lack of fringe-fibrils on the walls of the hyaline cells of the branch-leaves, is more frequent than the species. *Blount, *Cumberland, Johnson, *Polk, *Roane, and *Sevier Counties.

4. *Sphagnum compactum* DC. Wet soil and rocks. Not common. *Morgan, *Roane, Sevier and Van Buren Counties.

5. *Sphagnum squarrosum* Crome. Wet rocks. Rare. Near the summit of Mt. LeConte, Sevier County. The southernmost known station in North America.

6. *Sphagnum subsecundum* Nees. Wet soils and rocks. Not common. Bledsoe, *Blount, *Cumberland, Marion, *Morgan, *Polk and *Scott Counties.

7. *Sphagnum Pylaeisii* Brid. Wet rocks. Rare. Near the summit of Mt. LeConte, Sevier County. Only the unbranched form has been collected.

8. *Sphagnum Girgensohnii* Russow. Wet rocks. Rare. Near the summit of Mt. LeConte, Sevier County. The southern-most known station in North America.

9. *Sphagnum capillaceum* (Weiss.) Schrank. Peat of "heath bald." Rare. Sevier County.

10. *Sphagnum quinquefarium* (Lindb.) Warnst. Wet rocks. Not common. *Cocke and Sevier Counties.

11. *Sphagnum tenerum* Sull. & Lesq. Wet rocks. Very infrequent. Cumberland and Fentress Counties.

12. *Sphagnum tabulare* Sull. Wet rocks. Very infrequent. *Roan and Van Buren Counties.

Class III. SCHIZOCARPAE (ANDREAEAE)

Only one order, *Andreaeales*, and one family, *Andreaeaceae*, in the order, and one genus, *Andreaea*, in our flora.

Andreaea (Ehrh.) Hedw.

KEY TO SPECIES

1. Leaves ecostate 1. *rupestris*
 1. Leaves costate 2. *Rothii*

1. *Andreaea rupestris* Hedw. On non-calcareous rocks. Rare. Sevier County.

2. *Andreaca Rothii* W. & M. On non-calcareous rocks. More frequent. Campbell, Carter, Cumberland, Hamilton, Morgan, Polk, Putnam and Sevier Counties.

Class IV. ODONTOCARPAE

KEY TO ORDERS¹

1. Sporangium without a columella, the sporogenous and vegetative cells commingled; spores very large; archegonium not forming a calyptra but finally rupturing irregularly; operculum and peristome none; seta and stomata none; small acrocarpous mosses Order I. ARCHIDIALES
1. Sporangium with a definite central columella, which may, however, in rare cases be absorbed; spores relatively minute; archegonium developing as a calyptra; mostly with an operculum and peristome, but some cleistocarpous; seta and stomata frequently present, size variable; acrocarpous or pleurocarpous 2
2. Peristome teeth thin, derived from the cell-walls of a single layer of cells, always transversely barred; sometimes entirely wanting 3
2. Peristome teeth cellular, rarely absent, if present derived from several layers of cells, not transversely barred, or, if faintly barred, then the capsule decidedly dorsiventral and zygomorphic Order VII. POLYTRICHALES
3. Peristome single, composed of two layers of plates formed by a deposit on the inner and outer surfaces of one of the original tangential cell walls, rarely wanting; usually acrocarpous mosses Order II. DICRANALES
3. Peristome double or sometimes wanting; plates of the outer surfaces of the teeth mostly in two rows separated by a zigzag line, the inner surfaces of the teeth consisting of a single row of plates; endostome thin and membranous, sometimes lacking 4
4. Endostome mostly imperfectly developed or sometimes wanting; thickening of outer surface of exostome teeth greater than that of the inner; mostly pleurocarpous mosses Order III. LEUCODONTALES
4. Peristome distinctly double and the endostome usually well developed, except in astomous groups; pleurocarpous or acrocarpous 5
5. Endostome segments absent or, when present, alternating with the teeth of the exostome; hypophysis lacking or minute; pleurocarpous or acrocarpous 6
5. Endostome processes when present, opposite the teeth of the exostome, either free or united with them, but the peristome sometimes entirely wanting; hypophysis sometimes highly developed; acrocarpous mosses Order VI. SPLACHNALES (FUNARIALES)
6. Cilia usually wanting; gametophyte usually flattened, the leaves inequilateral; alar cells not differentiated; calyptra usually mitriform; mostly pleurocarpous mosses Order IV. HOOKERIALES
6. Cilia usually present; gametophyte occasionally flattened, leaves variable in shape; calyptra cucullate; alar cells variable; pleurocarpous and acrocarpous mosses Order V. HYPNOBRYALES

Order I. ARCHIDIALES

Representatives of this order have not been found in Tennessee.

Order II. DICRANALES

KEY TO FAMILIES

1. Leaves in more than two rows on the stem 2
1. Leaves in two rows on the stem 9
2. Gametophyte gray-green, with colorless cells in the thick leaves II. LEUCOBRYACEAE
2. Gametophyte light green to almost black; leaves usually one cell in thickness; colorless cells infrequent 3
3. Calyptra covering the entire capsule VIII. ENCALYPTEACEAE
3. Calyptra not covering the entire capsule 4
4. Basal cells near the costa greatly enlarged VI. CALYMPERACEAE

¹ This key is adapted from the synopsis of Schaffner (1938b).

4. Basal cells near the costa not greatly enlarged 5
 5. Gametophyte dark, brownish, or blackish, growing on rocks; seta short, peristome-teeth red or brown, triangular-lanceolate, usually not deeply bifid at apex V. GRIMMIACEAE
 5. Gametophyte usually green, growing on various substrata; seta long or short; peristome-teeth variable in color and shape 6
 6. Gametophyte and sporophyte 1 cm. or less, found only on rocks; leaves smooth, usually awned (See also *Rhabdowesia*) IV. SELIGERACEAE
 6. Gametophyte and sporophyte usually exceeding 1 cm., found on various substrata; leaves frequently papillose, sometimes awned 7
 7. Gametophyte of most species with falcate-secund leaves; peristome-teeth usually triangular-lanceolate and bifid half their length I. DICRANACEAE
 7. Gametophyte of few species with falcate-secund leaves; peristome-teeth usually linear, or split to the base, or lacking, or the capsules astomous 8
 8. Leaf very slender; leaf-cells smooth III. DITRICHACEAE
 8. Leaf broad to slender depending on the species; leaf-cells usually papillose VII. TORTULACEAE
 9. Costa with a lamina-like dorsal wing; peristome present X. FISSIDENTACEAE
 9. Dorsal wing on the costa lacking or obscure; peristome absent IX. BRYOXIPHIACEAE

I. DICRANACEAE

KEY TO GENERA

1. Alar cells not conspicuously enlarged 2
 1. Alar cells conspicuously enlarged 6
 2. Leaf-cells papillose 3. OREOWEISIA
 2. Leaf-cells essentially smooth 3
 3. Leaf crisped when dry 4
 3. Leaf not crisped when dry 5
 4. Gametophyte less than 5 mm. high; capsule erect and not strumose 2. RHABDOWESIA
 4. Gametophyte more than 5 mm. high; capsule inclined and strumose 4. ONCOPHORUS
 5. Gametophyte pale, capitate with slender, fasciculate juvenile branches 8. BROTHERA
 5. Gametophyte darker green, unbranched or with ordinary branches 1. DICRANELLA
 6. Costa with bands of stereid cells 7
 6. Costa without bands of stereid cells 9. PARALEUCOBRYUM
 7. Costa relatively narrow; capsule with stomata 5. DICRANUM
 7. Costa relatively broad; capsule without stomata 8
 8. Leaves curved, often falcate-secund 6. DICRANODONTIUM
 8. Leaves straight or sometimes slightly contorted 7. CAMPYLOPUS

1. *Dicranella* Schimp.

KEY TO SPECIES

1. Capsule erect, symmetric 2. *rufescens*
 1. Capsule inclined, asymmetric 2
 2. Gametophyte less than 1 cm. high; seta red 1. *varia*
 2. Gametophyte larger than 1 cm.; seta yellow (occasionally dark with age) 3. *heteromalla*
 1. *Dicranella varia* (Hedw.) Schimp. On moist banks. Not common. Blount, Claiborne, *Fentress and Union Counties.
 2. *Dicranella rufescens* (Sm.) Schimp. On moist sandy banks. Uncommon. Morgan and Sevier Counties.
 3. *Dicranella heteromalla* (Hedw.) Schimp. On soil of various types. Very common. Blount, Carter, *Hamilton, Knox, and Sevier Counties.

2. *Rhabdowesia* B.S.G.

Rhabdowesia denticulata (Brid.) B.S.G. In crevices of siliceous rocks in elevated regions. Uncommon. Blount, Hamilton, *Morgan and Sevier Counties.

3. *Oreoweisia* De Not.

Oreoweisia serrulata (Funk.) De Not. On moist rocks. Known only from Abrams Falls, Blount County. Apparently more widely distributed northward.

4. *Oncophorus* Brid.

Oncophorus Raui (Aust.) Grout. On vertical surfaces of siliceous boulders and cliffs. Not common. Sevier County.

5. *Dicranum* Hedw.

KEY TO SPECIES

1. Gametophyte with flagelliform branches in the axils of the upper leaves...2. *flagellare*
1. Gametophyte without flagelliform branches 2
2. Leaf distinctly papillose beneath throughout distal half1. *montanum*
2. Leaf smooth beneath or papillose only near the apex 3
3. Gametophyte large; leaves strongly transversely undulate9. *rugosum*
3. Gametophyte smaller; leaf, if transversely undulate, not conspicuously so 4
4. Leaf ovate, widest near the middle6. *spurium*
4. Leaf oblong-lanceolate, widest at the base 5
5. Leaf falcate-secund, usually crisped; cells of the median portion of the leaf 1-3 times as long as wide 6
5. Leaf sometimes falcate-secund, seldom crisped; cells of the median portion of the leaf 5-8 times as long as wide 8
6. Capsule straight3. *fulvum*
6. Capsule curved 7
7. Gametophyte growing on sandy soil or rocks5. *condensatum*
7. Gametophyte growing on wood or peaty soil4. *fuscescens*
8. Leaf usually falcate-secund; apex slender7. *scoparium*
8. Leaf usually laxly spreading; apex broad, often obtuse8. *Bonjeani*

1. *Dicranum montanum* Hedw. On trees or decaying logs. Not uncommon. *Blount, Campbell, *Grainger, Knox, *Monroe, Sevier, Unicoi and Washington Counties.

2. *Dicranum flagellare* Hedw. On trees or decaying logs. Common. Blount, *Cocke, *Roan, *Scott, Sevier, *Unicoi, Washington and Wilson Counties.

3. *Dicranum fulvum* Hook. On steeply sloping faces of siliceous boulders and cliffs. Common in the mountains. *Anderson, *Blount, Carter, Johnson and Sevier Counties. The variety *viride* (S. & L.) Grout, is found on exposed tree roots, trunks and logs. Not common. Campbell and Johnson Counties.

4. *Dicranum fuscescens* Turn. On trees and logs. Rare except on high mountain tops. *Blount and Sevier Counties.

5. *Dicranum condensatum* Hedw. On siliceous rocks and in very sandy soil. Not uncommon. Blount, Campbell, *Grainger, Knox, Marion, Polk, Putnam, Sevier and Van Buren Counties.

6. *Dicranum spurium* Hedw. On dry sandy soils. Uncommon. Campbell, Cumberland, *Fentress and Grainger Counties.

7. *Dicranum scoparium* Hedw. On various soils. One of our commonest mosses. Anderson, Blount, Campbell, Carter, Cheatham, Cocke, Cumberland, *Davidson, Hamilton, *Hancock, Knox, *Loudon, *Morgan, Sevier and Union Counties.

8. *Dicranum Bonjeani* De Not. On various soils. Uncommon. Blount, Johnson, Knox and Polk Counties.

9. *Dicranum rugosum* (Hoffm.) Brid. (*D. undulatum* Ehrh.) On soil in pine woods. Rare. Anderson and Knox Counties.

6. *Dicranodontium* B.S.G.

KEY TO SPECIES

1. Leaf never serrulate in the lower half, often caducous1. *denudatum*
1. Leaf serrulate to the base, never caducous 2. *asperulum*

1. *Dicranodontium denudatum* (Brid.) E. G. Britt. On siliceous boulders and cliffs in the mountains. Uncommon. Blount, *Morgan and Sevier Counties.

2. *Dicranodontium asperulum* (Mitt.) Broth. On siliceous boulders and cliffs in the mountains. Uncommon. Carter, Morgan and Sevier Counties.

7. *Campylopus* Brid.

KEY TO SPECIES

1. Leaf without conspicuous lamellae; apex not prolonged into a hair.....1. *tallulensis*
 1. Leaf with lamellae on its lower surface near apex, usually piliferous.....2. *introflexus*

1. *Campylopus tallulensis* Sull. & Lesq. On siliceous rocks or soil. Uncommon. Campbell, Fentress, Hamilton, Sevier and Unicoi Counties.

2. *Campylopus introflexus* (Hedw.) Brid. On siliceous rocks. Rare. Sevier and Van Buren Counties.

8. *Brothera* C. Muell.

Brother Leana (Sull.) C. Muell. On decaying wood and tree trunks. Rare. Knox and Sevier Counties.

9. *Paraleucobryum* (Lindb.) Loeske

Paraleucobryum longifolium (Hedw.) Loeske. (*Dicranum longifolium* Ehrh.) On trees in high mountains. Rare. Carter, *Cocke, and Sevier Counties.

II. LEUCOBRYACEAE

Leucobryum Hampe

KEY TO SPECIES

1. Gametophyte generally over 2 cm. long; upper tubular part of leaf longer than the flattened basal portion1. *glaucum*
 1. Gametophyte generally less than 2 cm. long; upper tubular part of leaf shorter than the flattened basal portion.....2. *albidum*

1. *Leucobryum glaucum* (Hedw.) Schimp. On soil and moist cliffs. Not uncommon. Blount, Cocke, *Fentress, Grainger, Hamilton, Knox, Morgan, *Polk, Union and *Washington Counties.

2. *Leucobryum albidum* (Brid.) Lindb. On soil, stumps and logs. Not uncommon. Blount, Hamilton, *Loudon, Morgan, Sevier and *Unicoi Counties.

III. DITRICHACEAE

KEY TO GENERA

1. Capsule dehiscing irregularly, without operculum or peristome 2
 1. Capsule with an operculum and peristome 3
 2. Capsule ovoid, without a conspicuously differentiated neck 1. *PLEURIDIUM*
 2. Capsule pyriform or long-necked 2. *BRUCHIA*
 3. Capsule with a long, slender basal neck 3. *TREMATODON*
 3. Capsule without a conspicuously differentiated base 4
 4. Capsule sulcate, dark purplish-brown 4. *CERATODON*
 4. Capsule not sulcate, generally of a lighter color 5. *DITRICHUM*

1. *Pleuridium* Brid.

KEY TO SPECIES

1. Calyptra mitrate; stomata near the middle of the capsule-wall.....3. *palustre*
 1. Calyptra cucullate; stomata basal 2
 2. Perichaetial leaf abruptly narrowed into a long subulate point; plants usually 3-5 mm. high 1. *subulatum*
 2. Perichaetial leaf gradually narrowed into a subulate point; plants usually 2-3 mm. high 2. *acuminatum*

1. *Pleuridium subulatum* (Hedw.) Lindb. (*P. alternifolium* of authors). On sandy soil. Not common. Grainger and Knox Counties.

2. *Pleuridium acuminatum* Lindb. [*P. subulatum* (Huds.) Rabenh.] On sandy soil. Not common. Grainger and *Union Counties.

3. *Pleuridium palustre* (B. S. G.) B. S. G. On wet soils. Rare. Johnson County.

2. *Bruchia* Schwaegr.

KEY TO SPECIES

1. Neck of capsule about the length of the spore-producing region1. *Sullivanti*

1. Neck of capsule very short, at times almost inconspicuous 2. *flexuosa*

1. *Bruchia Sullivanii* Aust. On sandy soil. Rare. Grainger County.

2. *Bruchia flexuosa* (Sw.) C. Muell. On sandy soil. Rare. *Grainger County.

3. *Trematodon* Mx.

Trematodon longicollis Mx. On sandy trailside banks. Rare. Blount and Sevier Counties.

4. *Ceratodon* Brid.

Ceratodon purpureus (Hedw.) Brid. On various substrata, more frequently on charcoal and substrata containing calcium salts. Very common. *Anderson, Blount, Carter, *Grainger, *Hamilton, Johnson, *Knox, Lincoln, *Marion, Rutherford, Sevier, *Unicoi and Washington Counties.

5. *Ditrichum* (Timm) Hampe

KEY TO SPECIES

1. Seta of sporophyte bright yellow 3. *pallidum*

1. Seta of sporophyte red to brown 2

2. Awn of perichaetial leaf as long as the widened base 1. *pusillum*

2. Awn of perichaetial leaf much shorter than the sheathing base 2. *lineare*

1. *Ditrichum pusillum* (Hedw.) E. G. Britt. (*D. tortile* Brockm.) Moist bare soil. Not uncommon. *Campbell, Carter, Cumberland, Knox, Morgan, Sevier, Sullivan and Union Counties.

2. *Ditrichum lineare* (Sw.) Lindb. [*D. vaginans* (Sull.) Hampe]. On bare soil. Rare. Marion and *Carter Counties.

3. *Ditrichum pallidum* (Hedw.) Hampe. On dry banks and old fields. Common. *Blount, Grainger, Greene, Knox, *Polk, Sevier, *Union, and Washington Counties.

A collection evidently representing a new species has been made in Van Buren County. Better material of this moss has since been collected in Ohio, and the disposition of the species is in the hands of Mr. R. T. Wareham of the Ohio State University.

IV. SELIGERIAEAE

KEY TO GENERA

1. Alar cells of leaves not enlarged 1. *SELIGERIA*

1. Alar cells of leaves enlarged 2. *BLINDIA*

1. *Seligeria* B.S.G.

Seligeria Doniana (Smith) C. Muell. On siliceous boulders at a high altitude. Sevier County. Collected only once. Its center of distribution is in Canada.

2. *Blindia* B.S.G.

Blindia acuta (Hedw.) B. S. G. On moist cliffs and boulders at high altitudes. Sevier County. Rare. Its distribution is similar to that of the preceding species.

V. GRIMMIAEAE

KEY TO GENERA

1. Leaf-cells not sinuose or sinuose only in the basal portion of the leaf 1. *GRIMMIA*

1. Leaf-cells sinuose throughout most of the leaf 2. *RHACOMITRIUM*

1. *Grimmia* Hedw.

KEY TO SPECIES

1. Apical hair of leaf none or short 2

1. Apical hair present, over 1/3 as long as the rest of the leaf 5

2. Leaf with costa prominently convex on the dorsal surface; margin strongly thickened 1. *teretiuscula*

2. Leaf without conspicuously terete costa; margin not strongly thickened 3

3. Leaf often with short apical hair, obscurely serrate; costa papillose beneath in distal portion 4. *gracilis*

3. Leaf not serrate; costa not noticeably papillose 4

4. Leaf muticous (var. *rivularis*) 2. *alpicola*
 4. Leaf acute, often with short, apical hair 3. *apocarpa*
 5. Base of apical hair not noticeably flattened nor decurrent 6. *Olneyi*
 5. Base of apical hair flattened and decurrent 7. *laevigata*
1. *Grimmia teretineris* Limpr. On limestone. Rare. *Knox County. Known elsewhere in North America from Idaho, Minnesota and Ontario.
 2. *Grimmia alpicola* Hedw. Only the variety *rivularis* (Brid.) Broth., is known in Tennessee. Uncommon. Blount County.
 3. *Grimmia apocarpa* (L.) Hedw. On dry rocks. Common. *Blount. *Campbell, Davidson, *Grainger, Knox and Sevier Counties.
 The variety *conferta* (Funck.) Spreng., is known from Roane County.
 4. *Grimmia gracilis* Schleich. On siliceous rocks. Uncommon. Blount and Sevier Counties.
 5. *Grimmia pilifera* Beauv. On siliceous rocks. Not common. *Blount, Campbell, *Fentress, *Hamilton, *Roane and *Sevier Counties.
 6. *Grimmia Olneyi* Sull. On siliceous rocks. Rare. Grainger County.
 7. *Grimmia laevigata* (Brid.) Brid. [*G. campestris* (Hook.) Bursch.; *G. leucophaea* Grev.]. On siliceous rocks. Not common. Campbell, Cocke, Fentress, *Grundey, Unicoi and Van Buren Counties.

2. *Racomitrium* Brid.

KEY TO SPECIES

1. Leaf with broad, obtuse apex 1. *aciculare*
 1. Leaf with slender, acute apex 2. *heterostichum*
1. *Racomitrium aciculare* Brid. On boulders in brooks. Uncommon. *Knox, *Roane and Sevier Counties.
 2. *Racomitrium heterostichum* (Hedw.) Brid. The variety *sudeticum* (Funck) Jones, is found on rocks of mountain tops. Uncommon. Carter County.
 The variety *ramulosum* (Lindb.) Jones, known by the elongated upper leaf cells, is found in similar situations. Rare. Sevier County.

VI. CALYPERACEAE

Syrrophodon Schwaegr.

- Syrrophodon texanus* Sull. On vertical surfaces of sandstone bluff. Rare. Fentress County. Widely distributed in the southern Coastal Plain.

VII. TORTULACEAE

KEY TO GENERA

1. Leaf usually narrow, often linear-lanceolate, not broadest above the middle; margin if differentiated, never so above the middle 2
 1. Leaf usually broad, ovate-oblong, spatulate or lingulate, sometimes differentiated 16
 2. Most of the basal leaf-cells chlorophylliferous 1. *Anoetangium*
 2. All, or at least the outer, basal leaf-cells hyaline, pellucid or yellow 3
 3. Hyaline, basal cells extending up the margin in a distinct band 4
 3. Hyaline, basal cells not extending up the margin in a distinct band 5
 4. Median basal cells colored, short, firm; lateral basal cells hyaline; leaf somewhat serrate above; finely papillose 11. *Pleurochaete*
 4. Median basal cells similar to internal basal cells, not chlorophylliferous; leaf not serrate; coarsely papillose 10. *Tortella*
 5. Leaf involute 6
 5. Leaf not involute 8
 6. Leaf broadly pointed; costa 60 microns or more in width at the base, reddish 7. *Hymenostomum*
 6. Leaf narrowly pointed; costa 50-60 microns in width at the base, not reddish or only slightly so 7
 7. Basal leaf-cells (especially of the upper leaves) 5-10 times as long as wide; upper leaf-cells distinct; sporophyte immersed 3. *Astomum*

1 The keys of this family are adapted from those of Wingo (1936).

7. Basal leaf-cells (especially of the upper leaves) 2-6 times as long as wide; upper leaf-cells dense and indistinct; sporophyte exserted 4. WEISIA
8. Leaf long, 2-3 mm., often reaching 4 mm., strongly papillose above; margin undulate and often sinuose 9. TRICHOSTOMUM
8. Leaf not generally longer than 2 mm.; margin plane or revolute 9
9. Leaf-margin serrate either distally or proximally by projecting cells 10
9. Leaf-margin entire 11
10. Margin toothed just above the base for a short distance; basal leaf-cells 5-10 times as long as wide, hyaline 8. EUCLADIUM
10. Margin serrate near apex, not below; basal cells less than 5 times as long as wide, yellowish 12. LEPTODONTIUM
11. Leaf-margin plane (*Barbula convoluta* almost so, slightly recurved at base) 12
11. Leaf-margin recurved at base or along one side 13
12. Leaf not crisped when dry; peristome lacking 5. GYMNSTOMUM
12. Leaf crisped when dry; peristome of 32 filiform teeth BARBULA CONVOLUTA Hedw.
13. Margin revolute near the middle; stem not more than 2 mm. high; leaf piliferous; sporophyte immersed 16. PHASCUM
13. Margin revolute near the base or along one side; stem more than 2 mm. high; leaf not piliferous; sporophyte exserted 14
14. Stem sparsely radiculose, never tinged with reddish-brown, triangular in cross-section; upper leaf-cells distinct; papillae low and few; peristome lacking 6. HYMENOSTYLIIUM
14. Stem radiculose, often tinged with reddish-brown, never triangular in cross-section; upper leaf cells papillose (not strongly so in *Didymodon*); peristome of 16 or 32 teeth 15
15. Plants often coated below with calcareous matter, whitish; upper leaves short, obtuse-ligulate; costa ending below apex; leaf-cells slightly papillose distally; peristome of 16 teeth, more or less divided or perforate along the median line, erect or twisted to the right 14. DIDYMODON
15. Plants not coated as above; upper leaves not as above; costa ending below apex or excurrent; leaf-cells strongly papillose distally; peristome of 32 filiform teeth, strongly twisted to the left 15. BARBULA
16. Gametophyte with axillary, stalked gemmae 13. HYOPHILA
16. Gametophyte without axillary, stalked gemmae 17
17. Leaf with evident papillae or propagula or both; peristome of filiform teeth 18. TORTULA
17. Leaf without evident papillae or propagula; peristome none 18
18. Costa subpercurrent; leaf-margin often of slightly differentiated cells; growing on rocks 2. MERCEYA
18. Costa percurrent to slightly excurrent; leaf-margin never differentiated; growing on soil 17. POTTIA

1. *Anoetangium* Schw.

Anoetangium Peckii Sull. On moist rocks above 4500 feet in the Great Smoky Mountains. Rare. Sevier County. Known elsewhere only in the Catskill Mts. of New York.

2. *Merceya* Schimp.

Merceya ligulata (Spruce) Schimp. On moist rocks at high elevations. Rare. Sevier County. Known elsewhere in North America only in Arizona. In Europe, it is known from Salzburg, the Pyrenees and Switzerland.

3. *Astomum* Hamp.

Astomum Sullivantii B. S. G. On moist, clay banks, in pastures and crevices of limestone. Not common. Anderson, *Blount and Knox Counties.

4. *Hymenostomum* R. Br.

Hymenostomum tortile (Schw.) B.S.G. On dry calcareous rocks. Not common.

*Bledsoe, Grainger, Knox and Marion Counties. More common in southwestern United States.

5. *Weisia* Hedw.

Weisia controversa Hedw. Hedw. [*W. viridula* (L.) Hedw.] On banks, in pastures and crevices of rock. Common. *Anderson, *Blount, Davidson, *Grainger, *Hamilton, Knox, *Roane and Sevier Counties.

The variety, *stenocarpa* Nees, Hornsch. & Sturm, with its longer sporophyte, cylindrical capsule and longer, more perfect teeth has been found in Knox County.

6. *Gymnostomum* Hedw.

KEY TO SPECIES

1. Stem 1-10 mm. long; leaf lingulate-obtuse; spore-wall smooth; spores 8-10 microns in diameter 1. *calcareum*
1. Stem usually longer; leaf acute or subacute; spore-wall slightly roughened; spores 10-12 microns in diameter 2. *rupestre*

1. *Gymnostomum calcareum* Nees & Hornsch. On limestone rocks. Not common. Knox, Putnam, Roane and Washington Counties.

2. *Gymnostomum rupestre* Schleich. On moist siliceous rocks. Not common. Davidson, *Fentress, *Knox and Sevier Counties.

7. *Hymenostylium* Brid.

Hymenostylium recurvirostrum (Hedw.) Dix. On calcareous bluffs. Not common. Anderson, Knox, Roane and Sevier Counties.

8. *Eucladium* B.S.G.

Eucladium verticillatum (L.) B.S.G. On wet limestone rocks, near calcareous springs. Not common. Anderson, Knox, *Marion, Rutherford and Washington Counties. It has been more frequently collected in western North America.

9. *Trichostomum* Hedw.

Trichostomum tenuirostre Lindb. [*T. cylindricum* (Bruch) C. Muell.] On moist siliceous rocks. Not uncommon. Anderson, Blount, Cheatham, Hamilton, Knox, Putnam and Sevier Counties.

10. *Tortella* (C. Muell.) Limpr.

KEY TO SPECIES

1. Leaf long, linear-lanceolate, with a very acute apex 2
1. Leaf oblong-acuminate, obtusely acute, abruptly mucronate by the excurrent costa 1. *humilis*
2. Leaf twisted, crispate when dry, of one layer of cells throughout 2. *tortuosa*
2. Leaf erect, rigid, much less contorted when dry, of 2 layers of cells distally 3. *fragilis*

1. *Tortella humilis* (Hedw.) O. E. Jenn. [*T. caespitosa* (Schw.) Limpr.] On moist rocks, tree trunks and decaying logs. Common. Anderson, Blount, *Campbell, Cocke, Davidson, Grainger, *Grundy, Hamilton, Knox, Lincoln, Rutherford, Sevier, *Unicoi and Washington Counties.

2. *Tortella tortuosa* (L.) Limpr. In crevices of bluff. Rare. *Blount County.

3. *Tortella fragilis* (Drumm.) Limpr. Rare. On shale bluff along Emory River, Roane County.

11. *Pleurochaete* Lindb.

Pleurochaete squarrosa (Brid.) Lindb. On limestone and clay soil; restricted to cedar barrens. Uncommon. Davidson, Knox and Rutherford Counties.

12. *Leptodontium* Hamp.

Leptodontium excelsum (Sull.) E. G. Britt. (*Zygodon Sullivantii* C. Muell.) On bark of living *Abies Fraseri*. Rare. Carter and Sevier Counties. Known from Mexico and Central America.

13. *Hyophila* Brid.

Hyophila Tortula (Schw.) Hamp. [*H. riparia* (Aust.) Fleisch.] On moist rocks near springs and creeks; bluffs. Common in the Ridge and Valley Province. Anderson, Blount, *Campbell, Grainger, Hawkins, Knox and Marion Counties. More abundant toward the tropics.

14. *Didymodon* Hedw.1

Didymodon tophaceus (Brid.) Jur. On moist limestone bluff, often forming tufa. Rare. Knox County.

15. *Barbula* Hedw.

KEY TO SPECIES

1. Gametophyte with axillary propagula 3. *Cruegeri*
1. Gametophyte without axillary propagula 2
2. Leaf squarrose-recurved, reddish; stem reddish-brown 3
2. Leaf not squarrose-recurved; gametophyte light or dull yellowish-green 4
3. Leaves widely spaced along stem, strongly recurved, short-pointed 4. *reflexa*
3. Leaves closely arranged along stem, gradually acuminate, acute 2. *fallax*
4. Perichaetial leaf long, sheathing, convoluted; stem-leaf very slightly recurved along proximal margin, less than 3 mm. long 1. *convoluta*
4. Perichaetial leaf not convoluted, sheathing, or conspicuously different from the rest; stem-leaf margins recurved proximally; leaf generally over 3 mm. long 5. *unguiculata*
1. *Barbula convoluta* Hedw. On neutral soils, moist limestone and bricks. Not common. Blount, Hamilton and Knox Counties.
2. *Barbula fallax* Hedw. On moist rocks. Rare. Rutherford and Van Buren Counties.
3. *Barbula Cruegeri* Sond. On marble debris. Rare. Knox County. Reported by Sharp (1936a) as a form of *B. unguiculata*.
4. *Barbula reflexa* (Brid.) Brid. (*B. recurvifolia* Schimp.) On moist limestone rocks and soils. Uncommon. Blount, Knox and Marion Counties.
5. *Barbula unguiculata* Hedw. On clay banks, soils, rocks and bluffs. Common. Blount, Campbell, *Cocke, Davidson, *Hamilton, Knox, Marion and *Morgan Counties.

16. *Phascum* (L.) Hedw.

Phascum cuspidatum (Schreb.) Hedw. On moist, open soil. Only the variety *piliferum* (Schreb.) Hook. & Tayl., is known from Tennessee. Rare. Anderson and Knox Counties.

17. *Pottia* Fuern.

Pottia truncata (Hedw.) Fuern. On moist, open soil. Rare. Knox County. Previously not reported south of Pennsylvania.

18. *Tortula* Hedw.

KEY TO SPECIES

1. Marginal leaf-cells distinctly differentiated to form a border 7. *Porteri*
1. Marginal leaf-cells not distinctly differentiated to form a border 2
2. Gametophyte without propagula or gemmae 3
2. Gametophyte with propagula or gemmae 5
3. Leaf plane or only slightly revolute 2. *Egelingii*
3. Leaf strongly revolute 4
4. Costa excurrent into a smooth, hyaline hair—in length about $\frac{1}{2}$ that of the leaf; upper cells of the leaf 9-13 microns in diameter 3. *marialis*
4. Costa excurrent into a smooth, hyaline hair frequently as long as the leaf; upper cells 4-8 microns in diameter 6. *plinthobia*
5. Leaf not papillose; propagula beneath the basal portion of the leaves; propagula not papillose; costa disappearing above the middle of the leaf 7. *propagulosa*
5. Leaf papillose; propagula not limited to leaf bases; propagula papillose or smooth; costa percurrent or excurrent into a hair 6

1 Since the manuscript was completed *Didymodon rigidulus* Hedw. has been recorded from Blount Co.

6. Propagula flattened, terminal and surrounded by a lateral cup of leaves 4. *pagorum*
 6. Propagula cylindrical or globular, scattered on both surfaces of the leaf..... 7
 7. Propagula cylindrical; costa percurrent 1. *caroliniana*
 7. Propagula globular; costa often excurrent 5. *papillosa*

1. *Tortula caroliniana* Andrews. On conglomerate boulder. Rare. Sevier County. Originally described from North Carolina, it is rather widely distributed in Mexico and Central America.

2. *Tortula Egelingii* (Schlieph.) Broth. So far not reported from eastern Tennessee though originally described from Shelby County of western Tennessee by Schliephacke in Flora, 1887, page 222; it has not been reported since.

3. *Tortula muralis* Hedw. On moist stone and brick walls. Rare. Knox County.

4. *Tortula pagorum* (Milde) De Not. On tree trunks and limestone walls in towns or cities. Common in these areas. Greene, Jefferson, Knox, Marion and Washington Counties. Since this moss is not found far from habitation in the eastern United States it is perhaps adventive there.

5. *Tortula papillosa* (C. Muell.) Wils. On bark of elm in Greeneville. Rare. Greene County. Very recently collected by Dr. L. E. Anderson.

6. *Tortula plinthobia* (Sull.) Broth. On brick walls and rocks. Rare. Davidson and Knox Counties.

7. *Tortula Porteri* (James & Aust.) Broth. On brick walls and sandstone. Uncommon. Davidson, Knox, and Union Counties.

8. *Tortula propagulosa* Sharp. On the bark of elms in Knoxville. Rare. Knox County. Collected on three neighboring trees of *Ulmus americana* L., which are the only known stations.

VIII. ENCALYPTACEAE

Encalypta Schreb.

Encalypta contorta (Wulf.) Lindb. On calcareous rocks. Rare. Knox County.

IX. BRYOXIPHACEAE

Bryoxiphium Mitt.

Bryoxiphium norvegicum (Brid.) Mitt. On moist, vertical faces of conglomerate boulders and cliffs. Campbell and Fentress Counties. These counties are near the southern tip of its known range. For a discussion of its distribution, see Steere (1937b).

X. FISSIDENTACEAE

Fissidens Hedw.

KEY TO SPECIES

1. Gametophyte slender, aquatic 10. *Julianus*
 1. Gametophyte not aquatic (may be occasionally submerged) 2
 2. Leaf thick, opaque, two or more cells in thickness 9. *grandifrons*
 2. Leaf of a single layer of cells 3
 3. Leaf with at least a partial border of narrow, elongated cells 4
 3. Leaf without any evidence of a border of narrow, elongated cells 7
 4. Border vanishing below the apex, often limited to the lower half of the leaf 5
 4. Border reaching the apex, sometimes confluent with the costa 6
 5. Leaf apex obtuse, rounded 1. *obtusifolius*
 5. Leaf apex acute, pointed 2. *exiguus*
 6. Gametophyte usually less than 5 mm. tall; border of leaves comparatively thin 3. *minutulus*
 6. Gametophyte 5-25 mm. tall; border of leaves comparatively thick 4. *viridulus*
 7. Leaf bordered by several rows of paler, short cells 8. *cristatus*
 7. Leaf, if bordered by paler, short cells, with only a single row 8
 8. Costa excurrent into a short point 6. *taxifolius*
 8. Costa failing to reach the tip of the leaf 9
 9. Costa almost reaching the leaf apex; cells 17-20 microns in diameter 5. *osmundoides*
 9. Costa usually ending 8-10 cells below the leaf apex; cells 7-10 microns in diameter 7. *subbasilaris*

1. *Fissidens obtusifolius* Wils. On tree roots. Very rare. Claiborne County.

2. *Fissidens exiguus* Sull. On wet rocks. Uncommon. Blount, Hamilton, and Rutherford Counties.

3. *Fissidens minutulus* Sull. On moist rocks. Not uncommon. Blount, Cumberland, Knox and Washington Counties.

4. *Fissidens viridulus* (W. & M.) Wahlenb. On very wet rocks. Not common. Carter and Sevier Counties.

5. *Fissidens osmundoides* Hedw. On moist soil. Common. Blount, Campbell, Hamilton, Knox, Marion and Roane Counties.

6. *Fissidens taxifolius* Hedw. On moist soil. Common. Blount, Bradley, Davidson, Knox, Rutherford and Washington Counties.

7. *Fissidens subbasilaris* Hedw. On trees and rocks. Not uncommon. Blount, Campbell, Fentress, Grainger and Lincoln Counties.

8. *Fissidens cristatus* Wils. On moist soil and rocks. Very common. Anderson, Blount, Cheatham, Davidson, Grainger, Knox, Marion, Monroe, Putnam, Rutherford and Sevier Counties.

9. *Fissidens grandifrons* Brid. On wet limestone rocks. Not common. Campbell, Knox, Lincoln and Marion Counties.

10. *Fissidens julianus* (Mont.) Schimp. On rocks submerged in running water. Not common. Davidson, Hamilton, Knox, Marion and Rutherford Counties.

Order III. LEUCODONTALES

KEY TO FAMILIES

1. Cells in the distal portion of the leaf isodiametric 2
1. Cells in the distal portion of the leaf longer than wide 4
2. Leaf ecostate, papillose with forked papillae; perichaetial leaf with ciliate margin; capsule without peristome III. HEDWIGIACEAE
2. Leaf costate, if papillose, the papillae not forked; perichaetial leaf not ciliate at margin; capsule usually with peristome 3
3. Peristome always with linear-lanceolate teeth I. PTYCHOMITRIACEAE
3. Peristome absent or, if present, with triangular-lanceolate teeth II. ORTHOTRICHACEAE
4. Gametophyte slender, often $\frac{1}{2}$ -4 ft. long, aquatic IX. FONTINALACEAE
4. Gametophyte shorter, less than 6 inches in length, none strictly aquatic 5
5. Gametophyte dendroid in habit (obscure in *Climacium Kindbergii*) 6
5. Gametophyte not exhibiting a dendroid habit 7
6. Branches pointing in one direction like those of a wind-blown tree; gametophyte usually growing on vertical surfaces of moist, shaded rocks VII. POROTRICHACEAE
6. Branches divergent in several directions; gametophyte not growing on vertical surfaces of rocks VIII. CLIMACIACEAE
7. Gametophyte flattened until the leaves appear almost as if in two rows VI. NECKERACEAE
7. Gametophyte not flattened 8
8. Capsule immersed (in the perichaetial leaves) IV. CRYPHAEACEAE
8. Capsule emergent to exserted V. LEUCODONTACEAE

I. PTYCHOMITRIACEAE

KEY TO GENERA

1. Seta usually geniculate; calyptra plicate 1. CAMPYLOSTELIUM
1. Seta not geniculate; calyptra not plicate 2. PTYCHOMITRIUM

1. *Campylostelium* B.S.G.

Campylostelium saxicola (W. & M.) B.S.G. On siliceous rocks. Not common. Cheatham, Polk, Davidson and * Sevier Counties.

2. *Ptychomitrium* Fuern.

Ptychomitrium incurvum (Wahlenb.) Sull. On siliceous rocks. Uncommon. Blount, Carter, *Cocke, *Grainger, *Hamilton, *Knox, *Roane, Sevier and Van Buren Counties.

P. Drummondii Sull. has been collected in Lake County of western Tennessee.

II. ORTHOTRICHACEAE

KEY TO GENERA

1. Gametophyte prostrate, with numerous erect, short lateral branches 5
1. Gametophyte more or less erect 2
2. Gametophytes forming compact cushions on wet rocks 3. AMPHIDIUM

2. Gametophytes, if growing on rocks, not forming compact cushions 3
 3. Capsule not exerted 1. *ORTHOTRICHUM*
 3. Capsule plainly exerted 4
 4. Calyptra not hairy; plants found only on bark of fir 4. *ZYGODON*
 4. Calyptra hairy 2. *ULOTA*
 5. Capsule sub-spherical; peristome-teeth short, truncate 5. *DRUMMONDIA*
 5. Capsule much longer than broad; peristome-teeth slender, acute 6. *SCHLOTHEIMIA*

1. *Orthotrichum* Hedw.¹

KEY TO SPECIES

1. Gametophyte growing on rocks 2
 1. Gametophyte growing on trees 3
 2. Capsule sub-globose, abruptly contracted below 2. *Lescurii*
 2. Capsule sub-cylindrical, tapering below 1. *strangulatum*
 3. Leaf plainly denticulate at apex 6. *pusillum*
 3. Leaf entire or obscurely denticulate at apex 4
 4. Leaf with an acute apex 5. *pumilum*
 4. Leaf with an obtuse apex 5
 5. Capsule straw-colored, only slightly contracted below the mouth when dry and empty 4. *ohioense*
 5. Capsule darker, strongly plicate and contracted below the mouth when dry and empty 3. *stellatum*
 1. *Orthotrichum strangulatum* Schwaegr. (*O. Porteri* Aust.) On dolomitic rocks. Not common. Anderson, Davidson, Knox, Putnam and Washington Counties.
 2. *Orthotrichum Lescurii* Aust. On siliceous rock. Rare. Sevier County.
 3. *Orthotrichum stellatum* Brid. On various trees. Not very common. Blount, Carter, Knox, Sevier, Unicoi and Washington Counties.
 4. *Orthotrichum ohioense* S. & L. On various trees. Not very common. Anderson, Blount, *Cocke, Grainger, *Hamilton, Knox, Sevier and Washington Counties.
 5. *Orthotrichum pumilum* Dicks. On various trees. Uncommon. Knox and Sevier Counties.
 6. *Orthotrichum pusillum* Mitt. (*O. psilocarpum* James.) On various trees. Uncommon. Knox and *Washington Counties.

2. *Ulota* Mohr

KEY TO SPECIES

1. Leaf not crisped, scarcely contorted 1. *americana*
 1. Leaf contorted or crisped 2
 2. Capsule smooth except for the small, puckered mouth 2. *Ludwigii*
 2. Capsule strongly 8-ribbed 3. *crispa*
 1. *Ulota americana* (P.B.) Limpr. On siliceous rocks. Common in the mountains. *Blount, Carter, Cocke, Sevier and Washington Counties.
 Variety *rufescens* (E.G.B.) Paris, is found on beech trees above 4500 ft. in the Great Smoky Mountains. Sevier County.
 2. *Ulota Ludwigii* Brid. On deciduous trees in the mountains. Not common. *Blount, Carter and *Sevier Counties.
 3. *Ulota crispa* (Hedw.) Brid. On deciduous trees. Uncommon. Blount, Carter, Cocke, Johnson, Roane, Sevier and Van Buren Counties.

3. *Amphidium* (Nees) Schimp.

Amphidium Mougeotii (B.S.G.) Schimp. On moist cliffs. Not common. Blount and Marion Counties.

4. *Zygodon* Hook. & Tayl.

Zygodon viridissimus (Dicks.) Brown. (*Z. rufo-tomentosus* E. G. Britt.) On the bark of *Abies Fraseri* (Pursh) Poir. which is found only on our highest mountain tops. Carter and Sevier Counties.

5. *Drummondia* Hook.

Drummondia prorepens (Hedw.) O. E. Jenn. (*D. clavellata* Hook.) On the bark

¹ Since the manuscript was completed, *Orthotrichum obtusifolium* Brid. has been found in Knox Co.

of trees. Rather common. Blount, *Cocke, Grainger, Knox, Sevier, Union and *Washington Counties. Found once in Knox County on a rock.

6. *Schlotheimia* Brid.

Schlotheimia Sullivantii C. Muell. On trees. Rare. Blount and *Polk Counties. Widely distributed in the southern Coastal Plain and the tropics.

S. lancifolia Bartr. may be found in eastern Tennessee since it grows in western North Carolina.

III. HEDWIGIACEAE

Hedwigia Hedw.

Hedwigia ciliata (Ehrh.) Hedw. On dry non-calcareous rocks. *Anderson, Campbell, *Cocke, Cumberland, *Hamilton, Knox, Polk and Sevier Counties. In contrast to its usual habitat, it was found once on the base of an oak on House Mt., Knox County.

IV. CRYPHAEACEAE

Cryphaea Mohr

KEY TO SPECIES

1. Costa ending near the middle of the leaf 1. *glomerata*
1. Costa ending in the apex of the leaf 2. *nervosa*

1. *Cryphaea glomerata* Schimp. On bark of trees or shrubs. Common. Anderson, Blount, Grainger, Knox, Sevier, Van Buren and Wilson Counties.

2. *Cryphaea nervosa* B.S.G. On bark of trees. Not common. Anderson, Blount, Knox and Sevier Counties.

V. LEUCODONTACEAE

KEY TO GENERA

1. Secondary stems little branched; calyptra smooth 1. *LEUCODON*
1. Secondary stems profusely branched; calyptra hairy 2. *LEPTODON*

1. *Leucodon* Schwaegr.

KEY TO SPECIES

1. Seta shorter than the perichaetial leaves 1. *brachypus*
1. Seta longer than the perichaetial leaves 2
2. Stem-leaf slenderly acuminate, strongly plicate 2. *sciuroides*
2. Stem-leaf abruptly short-acuminate, scarcely plicate 3. *julaceus*

1. *Leucodon brachypus* Brid. On trees. Not very common. Blount, Knox, Scott and Sevier Counties.

2. *Leucodon sciuroides* (Hedw.) Schwaegr. On limbs of trees. Rare. Sevier County.

3. *Leucodon julaceus* (Hedw.) Sull. On trees. Common. Blount, Grainger, Hamilton, Knox, *Lincoln, Roane, Rutherford, *Unicoi, Van Buren, *Washington and Wilson Counties. Found once on a rock on House Mt. in Knox County.

2. *Leptodon* Mohr (*Forsstroemia* Lindb.)

Leptodon trichomitron (Hedw.) Mohr. Usually on trees but occasionally on rocks. Rather common. Anderson, *Blount, *Campbell, Knox, Roane and Sevier Counties.

VI. NECKERACEAE

KEY TO GENERA

1. Leaf not cultriform or lobed 1. *NECKERA*
1. Leaf cultriform or complicate-bilobed 2. *HOMALIA*

1. *Neckera* Hedw.

KEY TO SPECIES

1. Gametophyte growing on trees; leaf undulate 1. *pennata*
1. Gametophyte growing on rocks; leaf seldom undulate 2. *complanata*

1. *Neckera pennata* Hedw. On trees. Rather common in the high mountains. *Blount, Carter, *Cocke, Johnson and Sevier Counties.

2. *Neckera complanata* (Hedw.) Hueben. On bluffs. Not common. Blount, Cheatham, Knox, Marion, *Polk and Sevier Counties.

2. *Homalia* (Brid.) B.S.G.

KEY TO SPECIES

1. Leaf cultriform; not lobed 1. *Jamesii*
 1. Leaf not cultriform but with a small conduplicate lobe 2. *Sharpii*

1. *Homalia Jamesii* Schimp. On bluffs. Rare. Blount County.

2. *Homalia Sharpii* Williams. On vertical faces of dolomitic rocks. Rare. Anderson and Campbell Counties (type locality). This species is obviously related to *Homaliadelphus Targioniana* (Gough.) Dix. & Vard. of India, and should perhaps be transferred to that genus.

VII. POROTRICHACEAE

Porotrichum Brid.

Porotrichum alleghaniense (C. Muell.) Grout. On moist cliffs and boulders. Not very common. Anderson, Blount, *Cocke, Knox, *Marion, Putnam and Sevier Counties.

VIII. CLIMACIACEAE

Climacium Web. & Mohr

KEY TO SPECIES

1. Gametophyte distinctly dendroid; median leaf-cells 5-7 times as long as wide 1. *americanum*
 1. Gametophyte obscurely dendroid, often nearly prostrate; leaf-cells 2-3 times as long as wide 2. *Kindbergii*

1. *Climacium americanum* Brid. On soil, logs and rocks. Common. Anderson, Bledsoe, Blount, Cheatham, Cocke, Davidson, *Fentress, Grainger, Hamilton, *Knox, Morgan, Putnam, Sevier and Washington Counties.

2. *Climacium Kindbergii* (R. & C.) Grout. On wet soil and rocks. Not very common. *Anderson, Blount, Grainger, *Hamilton, Johnson, *Morgan, *Sevier, and *Washington Counties.

IX. FONTINALACEAE

1. Leaf ecostate 1. *Fontinalis*
 1. Leaf costate 2. *Dichelyma*

1. *Fontinalis* (L.) Myrin

KEY TO SPECIES

1. Leaves dimorphic, the stem- and branch-leaves being unlike with but little intergradation in shape or size 1. *Sullivantii*
 1. Leaves similar; stem- and branch-leaves intergrading 2
 2. Leaf-margin usually broadly involute 2. *dalecarlica*
 2. Leaf-margin only narrowly involute 3. *novae-angliae*

1. *Fontinalis Sullivantii* Lindb. On bushes in pond. Rare. Blount County. Most prevalent in the Coastal Plain.

2. *Fontinalis dalecarlica* B.S.G. On boulders in brooks. Rare. Sevier County.

3. *Fontinalis novae-angliae* Sull. On rocks in running calcium-free water. Rather common. Fentress, Grainger, Johnson, Marion, Morgan, *Polk and Sevier Counties. Variety *cymbifolia* (Aust.) Welch, with canaliculate leaves has been collected in Fentress, Marion and Morgan Counties.

Variety *Lorenziae* Card., with closely appressed, imbricate leaves has been collected in Grainger County.

2. *Dichelyma* Myrin

Dichelyma capillaceum (Brid.) Myrin. On decaying wood in a small pool. Very rare. Fentress County.

Order IV. HOOKERIALES

Only one family, *Hookeriaceae*, and one genus, *Hookeria*, in our flora.

Hookeria Sm.

Hookeria acutifolia Hook. (*H. Sullivantii* C. Muell.) On moist rocks in the mountains. Not very common. Blount, Campbell, Carter, Cumberland, Fentress, Monroe, *Morgan and Sevier Counties.

Order V. HYPNOBRYALES

KEY TO FAMILIES

1. Sporophyte lateral on primary stem or branch (pleurocarpous mosses) 2
1. Sporophyte terminal on main axis (acrocarpous mosses) 10
2. Leaf papillose but without projecting cell ends, except in *Herpetineurum* 3
2. Leaf smooth or papillose because of projecting cell-ends, except in *Schwetschkeopsis* 4
3. Gametophyte usually julaceous, light to glaucous green I. THELIACEAE
3. Gametophyte seldom julaceous, bright green to very dark II. LESKEACEAE
4. Capsule erect and symmetrical (*Hypnum imponens* may be sought here) 5
4. Capsule seldom erect, usually curved 6
5. Leaf costate, or if ecostate, then papillose III. FABRONIACEAE
5. Leaf ecostate and smooth IV. ENTODONTACEAE
6. Leaf ecostate or nearly so 7
6. Leaf costate, often doubly so except in *Campylium hispidulum* 8
7. Gametophyte complanate-foliate except in *Plagiothecium striatellum*; leaves seldom secund VII. PLAGIOTHECIACEAE
7. Gametophyte not complanate-foliate; leaves usually secund VIII. HYPNACEAE
8. Capsule usually ovoid, short, thick and asymmetrical, little contracted below the mouth when dry 9
8. Capsule usually longer, arcuate-cylindrical, somewhat contracted under the mouth when dry V. AMBLYSTEGIACEAE
9. Costa single and usually reaching beyond the middle of the leaf; paraphyllia none VI. BRACHYTHECIACEAE
9. Costa double and usually not so long; paraphyllia often abundant and large IX. HYLOCOMIACEAE
10. Leaf smooth 11
10. Leaf papillose 12
11. Leaf-cells longer than wide X. BRYACEAE
11. Leaf-cells nearly isodiametric XI. MNIAEACEAE
12. Capsule much longer than wide XII. AULACOMNIACEAE
12. Capsule subspherical, very short XIII. BARTRAMIACEAE

I. THELIACEAE

KEY TO GENERA

1. Paraphyllia present; segments of inner peristome rudimentary or lacking; cilia none 1. *Thelia*
1. Paraphyllia absent; segments of inner peristome well developed; cilia present 2. *Myurella*

1. *Thelia* Sull.

KEY TO SPECIES

1. Papillae on dorsal surface of leaf not branched 1. *hirtella*
1. Papillae on dorsal surface of leaf branched 2
2. Gametophyte growing on trees; leaf-margin ciliate 2. *asprella*
2. Gametophyte growing on sand or rocks; leaf-margin seldom ciliate 3. *Lescurii*

1. *Thelia hirtella* (Hedw.) Sull. On the base of trees. Common. *Anderson, Blount, Cocke, Cumberland, Grainger, Hamilton, *Knox, *Roane, Sevier and Washington Counties.

2. *Thelia asprella* Sull. On base of trees. Uncommon. Grainger and Knox Counties.

3. *Thelia Lescurii* Sull. On sand and sandstone. Rare. *Knox County.

2. *Myurella* B.S.G.

KEY TO SPECIES

1. Leaf obtuse, although often apiculate 1. *julacea*
1. Leaf more acute and acuminate 2. *Careyana*

1. *Myurella julacea* (Schwaegr.) B.S.G. On a shale bluff. Rare. Roane County, the southernmost station reported for this species. More frequent north of Pennsylvania and Colorado than in the Southern Appalachians.

2. *Myurella Careyana* Sull. In crevices of cliffs and bluffs. Not common. Blount, Knox, Putnam, Rutherford, Sevier and Washington Counties.

II. LESKEACEAE

KEY TO GENERA

1. Leaf papillose 2
 1. Leaf smooth 4. *HERPETINEURUM*
 2. Gametophyte with abundant paraphyllia; capsule curved 1. *THUIDIUM*
 2. Gametophyte with few or no paraphyllia; capsule erect and symmetric 3
 3. Sporophyte borne on a primary axis; paraphyllia sometimes present 2. *LESKEA*
 3. Sporophyte borne on a secondary axis; paraphyllia none 3. *ANOMODON*

1. *Thuidium* B.S.G.

KEY TO SPECIES

1. Apical cell of the branch-leaves with 2-4 papillae on the tip 2
 1. Apical cell of the branch-leaves with a single terminal papilla 6
 2. Paraphyllia numerous, large, frequently branched 3
 2. Paraphyllia few, small, usually unbranched 5
 3. Stems closely once-pinnate 3. *scitum*
 3. Stems bi- or tripinnate 4
 4. Leaf gradually acuminate; costa subpercurrent; perichaetial leaf ciliate 1. *delicatulum*
 4. Leaf broad, abruptly acuminate; costa subpercurrent, perichaetial leaf not ciliate 2. *recognitum*
 5. Branches smooth; plants small 4. *minutulum*
 5. Branches papillose; plants extremely small 5. *pygmaeum*
 6. Stem-leaf ovate, gradually acuminate 6. *microphyllum*
 6. Stem-leaf rounded-ovate, abruptly acuminate 7. *virginianum*

1. *Thuidium delicatulum* (Hedw.) Mitt. On moist soil, logs and rocks. Very common. Blount, Cocke, Cumberland, Grainger, Hamilton, *Knox, Sevier, *Unicoi and Washington Counties.

2. *Thuidium recognitum* (Hedw.) Lindb. On moist soil, logs and rocks, usually in calcareous regions. Not very common. Anderson, *Blount, *Johnson, Knox, Lincoln, Sevier and *Washington Counties.

3. *Thuidium scitum* (P. B.) Aust. On moist logs and rocks. Rare. Campbell County.

4. *Thuidium minutulum* (Hedw.) B.S.G. On moist logs and rocks. Not very common. Anderson, Blount, *Carter, Davidson, Knox and Sevier Counties. More prevalent in the southeastern states and the tropics than in the north.

5. *Thuidium pygmaeum* B.S.G. On moist bluffs and rocks. Not very common. *Anderson, Blount, Knox, Rutherford, Sevier and Washington Counties.

6. *Thuidium microphyllum* (Hedw.) Best. On rocks and in an abandoned greenhouse on wood. Rare. Knox County.

7. *Thuidium virginianum* (Brid.) Lindb. On soil. Not common. Blount, *Carter, Grainger, *Knox, Morgan and *Unicoi Counties.

2. *Leskea* Hedw.

KEY TO SPECIES

1. Leaf biplicate; margin often revolute 1. *gracilescens*
 1. Leaf not plicate; margin plane 2. *obscura*

1. *Leskea gracilescens* Hedw. On soil, bases of trees, on logs and rocks. Not very common. Davidson and Knox Counties.

2. *Leskea obscura* Hedw. On trees, logs, and occasionally on soil or rocks. Not very common. *Anderson, Blount, *Cocke, Knox and Sevier Counties.

3. *Anomodon* Hook. & Tayl.

KEY TO SPECIES

1. Branches slender, julaceus 2
 1. Branches coarse, seldom julaceous 3
 2. Leaf acute, apex piliferous 5. *rostratus*
 2. Leaf lingulate, obtuse, fragile 6. *tristis*

3. Gametophyte much branched; many branches flagelliform 4. *attenuatus*
 3. Gametophyte sparingly branched; without attenuate branches 4
 4. Leaf lingulate but conspicuously narrowed above; gametophyte growing on rocks 1. *viticulosus*
 4. Leaf lingulate but less narrowed above; gametophyte usually growing on trees or logs 5
 5. Leaf decurrent, without auricles, not apiculate 2. *minor*
 5. Leaf not decurrent, with large fimbriate-papillose auricles, often apiculate 3. *Rugelii*
 1. *Anomodon viticulosus* (Hedw.) Hook and Tayl. On calcareous bluffs and cliffs. Not very common. Anderson, *Campbell, Knox, Sevier and Washington Counties.
 2. *Anomodon minor* (P. B.) Lindb. On bases of trees, particularly those which have been inundated. Uncommon. *Blount and Knox Counties.
 3. *Anomodon Rugelii* (C. Muell.) Keissl. (*A. apiculatus* B.S.G.) On the trunks of deciduous trees in the mountains. Not very common. *Cocke and Sevier Counties. Mainly found in the Eastern Hemlock Region.
 4. *Anomodon attenuatus* (Schreb., Hedw.) Hueben. On moist rocks and bases of trees. Common. Anderson, *Blount, *Carter, Cheatham, Claiborne, *Hamilton, Hawkins, Knox, *Polk, Sevier, Union and Washington Counties.
 5. *Anomodon rostratus* (Hedw.) Schimp. On moist rocks and bases of trees. Common. Anderson, Blount, *Carter, *Cocke, Cumberland, Grainger, Hamilton, Knox, *Morgan, *Roane, *Sevier, Union and Washington Counties.
 6. *Anomodon tristis* (Cesati) Sull. Usually on trees; rarely on rocks. Rather common. Anderson, Blount, *Cocke, *Grainger, *Hamilton, Knox, *Morgan, Roane, Rutherford and Washington Counties.

4. *Herpetineurum* (C. Muell.) Card.
Herpetineurum toccocae (Sull. & Lesq.) Card. On conglomerate boulders. Rare. Sevier County. Indigenous in the tropics and in the Gulf coastal plain.

III. FABRONIACEAE

KEY TO GENERA

1. Gametophyte extremely small; leaf slightly denticulate to ciliate-dentate (occasionally entire) 1. *FABRONIA*
 1. Gametophyte larger; leaf entire to slightly denticulate 2
 2. Leaf costate 3
 2. Leaf ecostate 4. *SCHWETZCHKEOPSIS*
 3. Peristome single; gametophyte growing on trees or rocks 2. *CLASMATODON*
 3. Peristome double; gametophyte growing in knot-holes or in deep crevices of bark 3. *ANACAMPTODON*

1. *Fabronia* Raddi

KEY TO SPECIES

1. Leaf strongly serrate 1. *ciliaris*
 1. Leaf slightly denticulate to entire 2
 2. Leaf usually entire; peristome-teeth normal 2. *Ravenelii*
 2. Leaf frequently denticulate; peristome-teeth imperfect 3. *imperfecta*
 1. *Fabronia ciliaris* (Brid.) Brid. [*F. octoblepharis* (Schleich.) Schwaegr.] On rocks. Rare. *Carter and Sevier Counties.
 2. *Fabronia Ravenelii* Sull. (*F. caroliniana* S. & L.) On shale bluff. Rare. Blount County.
 3. *Fabronia imperfecta* Sharp. On elm trees. Rare. Knox County. Known only from the type locality.
 2. *Clasmatodon* Hook. & Wils.
Clasmatodon parvulus (Hampe) Sull. On bark and bluffs. Rather common. Anderson, Blount, *Cocke, Davidson, *Hamilton and Knox Counties.

3. *Anacamptodon* Brid.

Anacamptodon splachnoides (Froehl.) Brid. In knot-holes and deep crevices of bark. Rare. Blount, Carter, Knox and Sevier Counties.

4. *Schwetsckheopsis* Broth.

Schwetsckheopsis denticulata (Sull.) Broth. On bark of trees and on rocks. Not very common. Davidson, Morgan and Sevier Counties.

IV. ENTODONTACEAE

Entodon C. Muell.

KEY TO SPECIES

1. Leaf gradually and narrowly acuminate; segments of the inner peristome adherent to the teeth to the teeth of the outer 5. *brevisetus*
1. Leaf acute to apiculate; segments of inner peristome free 2
2. Leaves scarcely complanate 2. *seductrix*
2. Leaves strongly complanate 3
3. Seta yellow 4. *Drummondii*
3. Seta dark brown or red 4
4. Leafy stems and branches 1 mm. or more wide; peristome-teeth usually smooth 1. *cladorrhizans*
4. Leafy stems and branches less than 1 mm. wide; teeth of outer peristome striolate above 3. *Sullivantii*

1. *Entodon cladorrhizans* (Hedw.) C. Muell. On logs and bases of trees. Rare. Washington County.

2. *Entodon seductrix* (Hedw.) C. Muell. On soil, logs, rocks, and bases of trees. Common. Anderson, Blount, Cocke, Davidson, Grainger, Hamilton, Knox, *Lincoln, Sevier, *Unicoi and *Washington Counties.

3. *Entodon Sullivantii* (C. Muell.) Lindb. On moist rocks. Uncommon. Morgan, Sevier and Washington Counties.

4. *Entodon Drummondii* (B.S.G.) J. & S. On logs, bases of trees and on rocks. Not very common. Anderson, *Blount, *Grainger, Hamilton, Knox, *Morgan and *Sevier Counties. Prevalent in the southern coastal plain and Mexico. Probably identical with *E. macropodus* (Hedw.) C. Muell. of the West Indies.

5. *Entodon brevisetus* (Hook. & Wils.) J. & S. On the bark of trees. Rare. *Carter and Sevier Counties.

V. AMBLYSTEGIACEAE

KEY TO GENERA

1. Leaf-margin strongly differentiated 4. *SCIAROMIUM*
1. Leaf-margin not differentiated 2
2. Paraphyllia abundant and conspicuous 5. *CRATONEURON*
2. Paraphyllia not abundant or conspicuous 3
3. Leaves slender, strongly costate and falcate-secund 10. *DREPANOCLADUS*
3. Leaves not both strongly costate and falcate-secund 4
4. Leaf obtuse or rounded at the apex 5
4. Leaf acuminate and acute 6
5. Costa subpercurrent; gametophyte not conspicuously pinnately branched 8. *CALLIERGON*
5. Costa lacking or short and double; gametophyte large and pinnately branched 9. *CALLIERGONELLA*
6. Leaf-cells 2-5 times as long as wide 7
6. Leaf-cells 5-15 times as long as wide 8
7. Gametophyte amphibious; cell-walls not unusually thick; costa thin 2. *AMBLYSTEGIUM*
7. Gametophyte aquatic; cell-walls thick; costa thick and heavy 3. *HYGROAMBLYSTEGIUM*
8. Leafy shortly acuminate with obtuse apex 7. *HYGROHYPNUM*
8. Leaf more slenderly acuminate with acute apex 9
9. Leaves squarrose-spreading 6. *CAMPYLIUM*
9. Leaves erect-spreading or flaccid (See also *Campylium polygamum*). 1. *LEPTODICTYUM*

1. *Leptodictyum* (Schimp.) Warnst.

KEY TO SPECIES

1. Leaf broadly ovate to ovate-lanceolate, shortly acuminate; gametophyte some-

- times growing in wet places but not aquatic 2. *trichopodium*
 1. Leaf longer lanceolate, more slenderly acuminate; gametophyte usually aquatic 1. *riparium*

1. *Leptodictyum riparium* (Hedw.) Warnst. On rocks in water, often floating. Not very common. Anderson, Fentress, *Grainger, *Hamilton, Knox, Marion and Sevier Counties.

2. *Leptodictyum trichopodium* (Schultz.) Warnst. Only the variety *Kochii* (B.S.G.) Broth. is known in Tennessee. On moist soil. Uncommon. Carter, *Davidson and Knox Counties. It is doubtful that this plant merits varietal rank.

2. *Amblystegium* B.S.G.

KEY TO SPECIES

1. Costa usually ending shortly above the middle of the leaf 2
 1. Costa usually percurrent 3. *varium*
 2. Marginal cells at base of leaf quadrate or transversely elongate 1. *serpens*
 2. Marginal cells at base of leaf oblong or rectangular 2. *juratskanum*

1. *Amblystegium serpens* (Hedw.) B.S.G. On moist bases of trees, on logs, soil and rocks. Rare. Blount and Sevier Counties.

2. *Amblystegium juratskanum* Schimp. On moist substrata. Rare. Knox and Sevier Counties.

3. *Amblystegium varium* (Hedw.) Lindb. On moist substrata. Common. Bledsoe, *Blount, *Davidson, Grainger, *Hamilton, *Knox and Sevier Counties.

3. *Hygroamblystegium* Loeske

KEY TO SPECIES

1. Leaf with blunt apex; costa broad and only slightly attenuate 1. *tenax*
 1. Leaf acute; costa narrower and strongly attenuate 2. *orthocladon*

1. *Hygroamblystegium tenax* (Hedw.) O. E. Jenn. [*Hygroamblystegium irriguum* (Wils.) Loeske.] On very wet soil and rocks. Common. *Anderson, Blount, Davidson, Knox, Lincoln, *Roane, Sevier and Union Counties.

2. *Hygroamblystegium orthocladon* (P. B.) Grout. On wet rocks. Common. Anderson, *Davidson, Hamilton, Knox, *Marion, Rutherford and Sevier Counties.

4. *Sciaromium* Mitt.

Sciaromium Lescurii (Sull.) Broth. On wet rocks in mountain brooks. Not common. Blount, *Fentress, *Polk and Sevier Counties.

5. *Cratoneuron* (Sull.) Roth

Cratoneuron filicinum (Hedw.) Roth. On wet limestone. Rare. Campbell County.

6. *Campyllum* (Sull.) Mitt.

KEY TO SPECIES

1. Costa lacking or short 1. *hispidulum*
 1. Costa well developed 2
 2. Leaves squarrose 2. *chrysophyllum*
 2. Leaves often widely spreading but never squarrose 3
 3. Leaf gradually long-acuminate with an extremely long-channeled acumen 3. *polygamum*
 3. Leaf abruptly long-acuminate 4. *radicale*

1. *Campyllum hispidulum* (Brid.) Mitt. On base of trees and on logs. Rather common. Anderson, Blount, Cheatham, Grainger, Knox, Morgan, *Polk and Washington Counties. The manuals fail to note that the leaf may be lightly papillose on the dorsal surface of its proximal portion.

Variety *cordatum* Grout, with cordate, strongly serrulate leaves, has been collected in Knox County.

2. *Campyllum chrysophyllum* (Brid.) Bryhn. On moist soil and rocks. Common. *Anderson, Blount, Cheatham, Cocke, *Davidson, Grainger, *Hamilton, Knox, Rutherford, Sevier and Van Buren Counties.

Variety *brevifolium* (R. & C.) Grout, with falcate, secund, often serrulate leaves has been collected in Sevier County.

Variety *zemliae* (Jens.) Grout, with extremely slender leaves has also been collected in Sevier County.

3. *Campylium polygamum* (B.S.G.) Bryhn. On wet soil. Rare. Sevier County.

4. *Campylium radicale* (P.B.) Grout. On wet soil. Rare. *Grainger and Johnson Counties.

7. *Hygrohypnum* Lindb.

KEY TO SPECIES

- | | |
|---|---------------------------|
| 1. Cortical cells of stem enlarged, thin-walled and hyaline | 1. <i>ochraceum</i> |
| 1. Cortical cells of stem not so differentiated | 2 |
| 2. Costa single, reaching at least the middle of the leaf | 3 |
| 2. Costa short, double or forking, or absent | 4 |
| 3. Distal margins of leaf strongly involute | 2. <i>luridum</i> |
| 3. Distal margins of leaf scarcely involute | 3. <i>alpestre</i> |
| 4. Leaf broadly ovate to suborbicular | 5 |
| 4. Leaf lanceolate to broadly ovate-lanceolate | 6 |
| 5. Leaf small, very concave, entire | 5. <i>cochlearifolium</i> |
| 5. Leaf large, slightly concave, serrulate | 6. <i>dilatatum</i> |
| 6. Leaf denticulate in the distal portion | 7. <i>novae-caesareae</i> |
| 6. Leaf entire or denticulate only at apex | 7 |
| 7. Leaf entire, without enlarged alar cells | 2. <i>luridum</i> |
| 7. Leaf often serrulate, with enlarged alar cells | 4. <i>eugyrium</i> |

1. *Hygrohypnum ochraceum* (Turn.) Loeske. On wet rocks. Rare. *Sevier County.

2. *Hygrohypnum luridum* (Hedw.) Dix. [*H. palustre* (Hedw.) Loeske.] On wet rocks in the mountain brooks. Rare. Carter and Sevier Counties. This species reaches the southern limit of its known range in this area, and is more frequently found to the north.

3. *Hygrohypnum alpestre* (Hedw.) Loeske. On wet rocks in a mountain brook. Very rare. Blount County. Extremely rare in eastern North America. In addition to southeastern Canada and Newfoundland, it is known from Greenland, Alaska and British Columbia.

4. *Hygrohypnum eugyrium* (B.S.G.) Loeske. On wet rocks in mountain brooks. Not common, but more frequently found in this region than the other species of this genus. Blount, *Carter and Sevier Counties.

5. *Hygrohypnum cochlearifolium* (Vent.) Broth. On wet rocks in water falls of mountain brooks. Rare. Sevier County. As limited in its range as *H. alpestre*.

6. *Hygrohypnum dilatatum* (Wils.) Loeske. On wet rocks in mountain brooks. Rare. Sevier County.

7. *Hygrohypnum novae-caesareae* (Aust.) Grout. [*Sematophyllum micans* (Wils.) Braithw.] On moist rocks in the mountains. Not common. *Blount, *Cocke and Sevier Counties.

8. *Calliergon* (Sull.) Kindb.

Calliergon cordifolium (Hedw.) Kindb. On very wet soils and in pools. Rare. Johnson County. This moss reaches the southern limit of its known range in Tennessee.

9. *Calliergonella* Loeske

Calliergonella Schreberi (B.S.G.) Grout. On moist acid soils either over sandstone or under coniferous trees. Not rare. Anderson, *Blount, Carter, *Cocke, Cumberland, Knox, Sevier and Van Buren Counties.

10. *Depranocladus* (C. Muell.) Roth

KEY TO SPECIES

- | | |
|---|-----------------------|
| 1. Leaf entire; annulus present | 1. <i>Sendtneri</i> |
| 1. Leaf serrulate; annulus absent | 2. <i>exannulatus</i> |

1. *Depranocladus Sendtneri* (Schimp.) Warnst. On wet rocks. Rare. Sevier County.

2. *Depranocladus exannulatus* (Guemb.) Warnst. On moist soil. Rare. Sevier County.

VI. BRACHYTHECIACEAE

KEY TO GENERA

1. Leaf conspicuously papillose beneath by projecting cell-angles 2. BRYHNIA
1. Leaf not conspicuously papillose beneath (often slightly so in *Pseudisothecium*) 2
2. Leaf plicate, with subuliform apex 6. HOMALOTHECIUM
2. Leaf seldom plicate or, if so, never with subuliform apex 3
3. Leaf large, concave, spoon-shaped, abruptly acuminate 4. CIRRHYPHYLLUM
3. Leaf seldom spoon-shaped or, if so, more gradually acuminate 4
4. Apical cells of branch-leaf often shorter and broader than the rest; costa often ending in a spine beneath; operculum long-rostrate 3. EURHYNCHIMUM
4. Apical cells of branch-leaf not noticeably different; costa not ending in a spine beneath; operculum conic to conic-rostrate 5
5. Gametophyte small; calyptra hairy; inner peristome adherent to outer; seta rough 7. HOMALOTHECIELLA
5. Gametophyte larger; calyptra smooth; inner peristome separate from outer; seta smooth or rough 6
6. Leaf often slightly papillose beneath, with a large area of small, thick-walled, rounded alar-cells 1. PSEUDISOTHECIUM
6. Leaf not papillose; alar-cells not so conspicuously different, usually larger and thin-walled 5. BRACHYTHECIUM

1. *Pseudisothecium* Grout

Pseudisothecium myosuroides (Brid.) Grout. On boulders and cliffs in the high mountains. Rare. Sevier County. In North America apparently restricted to the Appalachian Mountains.

2. *Bryhnia* Kaurin

KEY TO SPECIES

1. Branch-leaf broad, shortly acuminate; apex twisted 1. *novae-angliae*
1. Branch-leaf ovate-lanceolate, more slenderly acuminate; apex not twisted 2. *graminicolor*
1. *Bryhnia novae-angliae* (Sull. & Lesq.) Grout. On wet soil and rocks. Not common. *Blount, *Cocke and Sevier Counties.
2. *Bryhnia graminicolor* (Brid.) Grout. On cliffs and rocks. Not uncommon. *Anderson, Blount, Cheatham, Davidson, Grainger, *Knox, Marion, Putnam and Sevier Counties.

3. *Eurhynchium* B.S.G.

KEY TO SPECIES

1. Gametophyte complanate-foliate; seta smooth 4. *serrulatum*
1. Gametophyte not complanate-foliate; seta smooth or rough 2
2. Gametophyte large, aquatic, growing in brooks or springs 3. *riparioides*
2. Gametophyte smaller, not aquatic 3
3. Seta smooth 2. *pulchellum*
3. Seta rough 1. *hians*
1. *Eurhynchium hians* (Hedw.) J. & S. [*Oxyrrhynchium hians* (Hedw.) Loeske.] On moist banks. Common. Anderson, Campbell, *Carter, Davidson, *Grainger, Hamilton, Knox, Lincoln and Sevier Counties.
2. *Eurhynchium pulchellum* (Hedw.) O. E. Jenn. [*E. strigosum* (Brid.) B.S.G.] On bases of trees, on logs and soil. Not common. Carter, *Grainger, Hamilton and Sevier Counties.
3. *Eurhynchium riparioides* (Hedw.) Sharp [*E. rusciforme* (Neck.) Mildé; *Platyhypnidium rusciforme* (Neck.) Fleisch.] On rocks in brooks or springs. Not uncommon. Blount, *Carter, *Cocke, *Fentress, *Grainger, Marion, Rutherford and Sevier Counties.
4. *Eurhynchium serrulatum* (Hedw.) Kindb. [*Rhynchostegium serrulatum* (Hedw.) J. & S.] On soil. Common. Anderson, Blount, Carter, *Cocke, Davidson, Grainger, *Hamilton, Rhea, *Roane, Sevier and Union Counties.

4. *Cirriphyllum* Grout

1. Leaf with a long, filiform acumination 1. *piliferum*
 1. Leaf shortly acuminate 2. *Bosci*

1. *Cirriphyllum piliferum* (B.S.G.) Grout. On soil. Uncommon. Campbell, Putnam and Sevier Counties.

2. *Cirriphyllum Boscii* (Schwaegr.) Grout. On soil. Common. Blount, *Cocke, *Davidson, Hamilton, Knox, Lincoln, Morgan, Polk, Putnam, *Scott, Sevier, Union, Washington and Wilson Counties.

5. *Brachythecium* B.S.G.

KEY TO SPECIES

1. Seta rough, at least toward the top 2
 1. Seta smooth throughout 4
 2. Seta rough throughout 3
 2. Seta rough above, smooth below 6. *plumosum*
 3. Enlarged alar cells numerous 5. *rivulare*
 3. Enlarged alar cells absent 4. *rutabulum*
 4. Branch-leaf broadly ovate, usually 1 mm. or less in length 3. *digastrum*
 4. Branch-leaf less broadly ovate, usually more than 1 mm. in length 5
 5. Capsule 2-3 times as long as wide, asymmetric and cernuous 1. *salebrosum*
 5. Capsule 3-4 times as long as wide, cylindrical, sub-erect 2. *oxycladon*

1. *Brachythecium salebrosum* (Hoffm.) B.S.G. On logs, bases of trees and on soil. Not common. Blount, Campbell, *Morgan, and Sevier Counties.

2. *Brachythecium oxycladon* (Brid.) J. & S. On soil, roots of trees and on rocks. Not uncommon. Anderson, Cheatham, *Knox, *Loudon, Sevier and Union Counties.

3. *Brachythecium digastrum* C. Muell. & Lindb. On rocks. Rare. Sevier County. Probably not more than a variety of *B. oxycladon*.

4. *Brachythecium rutabulum* B.S.G. On wet soil. Rare. Johnson County. This moss reaches the southern end of its known range in eastern Tennessee.

5. *Brachythecium rivulare* B.S.G. On very moist rocks and soil. Not uncommon. *Anderson, *Blount, Johnson, Knox, *Morgan and Sevier Counties.

6. *Brachythecium plumosum* (Hedw.) B.S.G. On wet rocks. Common. Blount, Carter, *Cocke, Morgan, Roane and Sevier Counties.

6. *Homalothecium* B. S. G.

Homalothecium Bonplandii (Hook.) J. & S. On dolomitic bluffs. Rare. Anderson and Marion Counties. Tropical. The only other station known for it in the United States is in Texas.

7. *Homalotheciella* Cardot

KEY TO SPECIES

1. Leaf abruptly long-acuminate 1. *subcapillata*
 1. Leaf gradually narrowed into a subfiliform acumination 2. *fabrofolia*

1. *Homalotheciella subcapillata* (Hedw.) Card. On bark of trees. Common. Anderson, Blount, *Cocke, *Grainager, *Hamilton, Knox and Sevier Counties.

2. *Homalotheciella fabrofolia* (Grout) Broth. On bark of trees. Rare. Johnson County.

VII. PLAGIOTHECIACEAE

Plagiothecium B. S. G.

KEY TO SPECIES

1. Axillary paraphyllia often present; leaf-cells in the distal portion sometimes papillose beneath 2
 1. Paraphyllia none; leaf-cells smooth 3
 2. Leaf-apex usually abruptly narrowed into an acumination; leaves overlapping 6. *deplanatum*
 2. Leaf-apex blunt; leaves seldom overlapping 7. *geophilum*
 3. Gametophyte relatively large; leaf decurrent 4
 3. Gametophyte small; leaf not decurrent 8
 4. Gametophyte not complanate-flattened 5

4. Gametophyte complanate-flattened 6
5. Leaves not squarrose; alar-cells not enlarged 4. *Roescanum*
5. Leaves squarrose; alar-cells enlarged 5. *striatellum*
6. Leaves usually shrinking on drying so that they do not overlap; gametophyte yellowish 2. *sylvaticum*
6. Leaves seldom shrinking on drying; gametophyte green 7
7. Leaf large, conspicuously decurrent; cilia of peristome 2 1. *denticulatum*
7. Leaf small, less decurrent; cilia of peristome 1 or none 3. *laetum*
8. Leaf entire; cortical cells of stem enlarged 8. *Muellerianum*
8. Leaf at least serrulate; cortical cells of stem not enlarged 9
9. Gametophyte pale green; costa faint or none 10. *micans*
9. Gametophyte darker green; costa usually evident 9. *elegans*

1. *Plagiothecium denticulatum* (Hedw.) B.S.G. On moist substrata in the mountains. Rather common. Blount, Carter, Sevier and Washington Counties.

2. *Plagiothecium sylvaticum* (Brid.) B.S.G. On moist rocks. Not common. Sevier County.

3. *Plagiothecium laetum* B.S.G. On bases of trees above 6000 feet. Rare. Sevier County.

4. *Plagiothecium Roescanum* (Hampe) B.S.G. On moist substrata. Not common. *Carter, *Morgan, and *Sevier Counties.

5. *Plagiothecium striatellum* (Brid.) Lindb. [*Dolicotheca striatella* (Brid.) Loeske]. On moist cliffs in the high mountains. Uncommon. Carter and Sevier Counties.

6. *Plagiothecium deplanatum* (Sull.) Grout. [*Taxiphyllum deplanatum* (Sull.) Fleisch.] On moist soil, bases of trees and on rocks. Not common. Fentress, Knox, Lincoln and Sevier Counties.

7. *Plagiothecium geophilum* (Aust.) Grout. [*Taxiphyllum geophilum* (Aust.) Fleisch.] On moist soil and rocks. Uncommon. *Anderson, Knox and Sevier Counties.

8. *Plagiothecium Muellerianum* Schimp. [*Isopterygium muellerianum* (Schimp.) Lindb.] On moist rocks in the mountains. Not common. Blount, *Carter, and Sevier Counties.

9. *Plagiothecium elegans* (Hook.) Sull. [*Isopterygium elegans* (Hook.) Lindb.] On moist siliceous rocks. Not common. Carter, *Morgan and Sevier Counties.

10. *Plagiothecium micans* (Sw.) Paris. [*Isopterygium micans* (Sw.) E. G. Britt.] On moist soil, bases of trees and logs. Not very common. *Blount, Hamilton, *Knox, Lincoln and Sevier Counties.

Variety *fulvum* Hook. & Wils., a more robust plant which turns brownish with age, has been found in *Blount County.

VIII. HYPNACEAE

KEY TO GENERA

1. Stem-leaves secund, often falcate (*Heterophyllum* may be found here) 2
1. Stem-leaves not falcate, rarely secund 6
2. Alar-cells enlarged, usually hyaline 3
2. Alar-cells not enlarged, frequently small and quadrate 5
3. Epidermis of capsule not collenchymatous 4
3. Epidermis of capsule collenchymatous 4. SEMATOPHYLLUM
4. Operculum long-rostrate 2. BROTHIERELLA
4. Operculum conical to short-rostrate 1. HYPNUM
5. Capsule erect, symmetric; segments of inner peristome at least partially adherent to outer peristome teeth; cilia absent or rudimentary 7. PYLAISIA
5. Capsule erect or more usually asymmetric; segments free; cilia usually well developed 1. HYPNUM
6. Capsule erect, symmetric; peristome without cilia 8. PLATYGURIUM
6. Capsule inclined to horizontal, usually curved; peristome with cilia 7
7. Alar-cells enlarged and hyaline 3. HETEROPHYLLIUM
7. Alar-cells not enlarged, often small and quadrate 8
8. Gametophyte very minute; leaves 0.8 mm. or less in length 6. AMBLYSTEGIELLA
8. Gametophyte of medium size; leaves about 1 mm. in length 5. HOMOMALLIUM

1. *Hypnum* Hedw.

KEY TO SPECIES

1. Alar cells conspicuously enlarged, hyaline and thin-walled 2
1. Alar cells not conspicuously enlarged, often smaller 3
2. Region of enlarged alar cells abruptly delimited from remaining leaf-cells 5. *Patentiae*
2. Region of enlarged alar cells gradually intergrading with remaining leaf-cells 6. *pratense*
3. Leaf papillose beneath with sharply projecting cell-ends 10. *molluscum*
3. Leaf not papillose 4
4. Gametophyte yellowish-green; beautifully plumose-pinnate; leaf plicate, apex curved toward the next lower branch 9. *Crista-castrensis*
4. Gametophyte seldom yellowish-green; pinnately or irregularly branched; leaf seldom plicate, apex curved toward the substratum 5
5. Capsule nearly erect and symmetric 6
5. Capsule curved, asymmetric, inclined or horizontal 7
6. Gametophyte relatively large; capsule 3-4 mm. long 1. *imponens*
6. Gametophyte relatively small; capsule less than 2 mm. long 8. *pallidum*
7. Quadrate alar cells very numerous 8
7. Quadrate alar cells few or none 9
8. Leaf usually entire, with a very few slightly enlarged alar cells 2. *cupressiforme*
8. Leaf serrate, with no enlarged alar-cells 7. *reptile*
9. Capsule when dry longitudinally plicate 3. *curvifolium*
9. Capsule when dry smooth or slightly wrinkled 4. *fertile*

1. *Hypnum imponens* Hedw. On moist logs, rocks and soil. Not uncommon. *Blount, *Cocke, *Johnson, *Knox, *Roane and Sevier Counties.

2. *Hypnum cupressiforme* Hedw. On moist soil. Rare. *Sevier County.

3. *Hypnum curvifolium* Hedw. On moist rocks, logs and soil. Common. *Anderson, Blount, Cocke, *Fentress, Hamilton, Johnson, Knox, *Morgan, *Roane, *Sevier, Union and Washington Counties.

4. *Hypnum fertile* Sendt. On moist logs. Not common. Blount, Carter, *Johnson and Sevier Counties. This species reaches the southern end of its known range in this region.

5. *Hypnum Patentiae* Lindb. (*H. arcuatum* Lindb.) On wet swampy soil. Rather common. Anderson, Carter, *Davidson, *Johnson, *Morgan, Rhea, Sevier and Union Counties.

Variety *elatum* Schimp. with the general appearance of *Drepanocladus* has been collected in Lincoln County.

6. *Hypnum pratense* Koch. On wet soils. Rare. *Blount County.

7. *Hypnum reptile* Mx. On base of trees and on logs and stones in the mountains. Uncommon. *Blount, Carter and Sevier Counties.

8. *Hypnum pallidum* (Hedw.) B.S.G. On bark of trees. Rare. *Sevier County. This and the preceding species reach the southern known limits of their eastern ranges in this region.

9. *Hypnum Crista-castrensis* Hedw. [*Ptilium Crista-castrensis* (Hedw.) De Not.] On moist humus, logs and rocks in the mountains. Uncommon. *Carter, *Cocke, Johnson and Sevier Counties. This is more frequently collected northward.

10. *Hypnum molluscum* Hedw. [*Ctenidium molluscum* (Hedw.) Mitt.] On moist banks, logs and rocks. Not common. *Blount, Campbell, Cheatham, Hamilton, *Johnson, Knox, Morgan and Sevier Counties.

2. *Brotherella* Loeske

KEY TO SPECIES

1. Gametophyte complanate-foliate; capsule asymmetric and inclined; cilia of peristome well developed 2
1. Gametophyte little complanate; capsule erect and symmetric; cilia none or rudimentary 3. *tenuirostris*
2. Gametophyte glossy, yellowish-green; operculum one-half as long as the

- rest of the capsule 1. *recurvans*
 2. Gametophyte not very glossy, seldom yellowish; operculum nearly as long
 as the rest of the capsule 2. *delicatula*
1. *Brotherella recurvans* (Mx.) Fleisch. On base of trees and on logs in the mountains. Not very common. Blount, Carter, *Cocke and Sevier Counties.
 2. *Brotherella delicatula* (James) Fleisch. On base of trees and on logs. Not common. *Cocke, *Johnson, *Knox, Marion, *Morgan and Sevier Counties.
 3. *Brotherella tenuirostris* (Schimp.) Broth. (*Hypnum cylindrocarpum* C. Muell.) On logs, soil and rocks. Uncommon. *Carter, Knox and Sevier Counties.

3. *Heterophyllum* (Schimp.) Kindb.

KEY TO SPECIES

1. Leaf entire 1. *Haldanianum*
 1. Leaf serrate 2. *nemorosum*
1. *Heterophyllum Haldanianum* (Grev.) Kindb. On moist soil. Extremely rare. *Blount County.
 2. *Heterophyllum nemorosum* (Koch) Kindb. On tree trunks, logs and rocks in the mountains. Not common. Blount, Johnson, Marion, *Morgan and Sevier Counties.

4. *Sematophyllum* Mitt.

KEY TO SPECIES

1. Gametophyte growing on trees or recently fallen logs; capsule nearly erect and symmetric 1. *adnatum*
 1. Gametophyte growing on rocks; capsule curved and asymmetric 2
 2. Leaf 1.5 mm. or less in length 2. *carolinianum*
 2. Leaf 2 mm. or more in length 3. *marylandicum*
1. *Sematophyllum adnatum* (Mx.) E. G. Britt. On bark of trees and recently fallen logs. Common. Anderson, Bledsoe, Blount, Cocke, Cumberland, Davidson, Hamilton, Knox, Marion and Sevier Counties.
 2. *Sematophyllum carolinianum* (C. Muell.) E. G. Britt. On moist rocks. Rather common. Blount, Cumberland, *Fentress, *Grainger, Hamilton, *Johnson, McMin, *Morgan, *Roane and Sevier Counties.
 3. *Sematophyllum marylandicum* (C. Muell.) E. G. Britt. On wet rocks. Uncommon. Cumberland, *Grainger, Hamilton and Sevier Counties.

5. *Homomallium* (Schimp.) Loeske

- Homomallium adnatum* (Hedw.) Broth. On rocks and bases of trees. Not common. Campbell, *Carter, Rhea and Sevier Counties

6. *Amblystegiella* Loeske

- Amblystegiella confervoides* (Brid.) Loeske. On moist rock. Not common. Anderson, *Campbell, Cheatham, *Knox, Rutherford and Van Buren Counties.

7. *Pylaisia* B.S.G.

KEY TO SPECIES

1. Segments of the inner peristome only partially adnate to the teeth of the outer peristome 1. *Selwyni*
 1. Segments of the inner peristome wholly adnate to the teeth of the outer peristome 2. *intricata*
1. *Pylaisia Selwyni* Kindb. On bark of trees. Uncommon. Anderson and Knox Counties. Found only at lower elevations in eastern Tennessee.
 2. *Pylaisia intricata* (Hedw.) B.S.G. On bark of trees. Uncommon. Blount, *Cocke and Sevier Counties. More frequent in our mountains than in the Valley and Ridge Province.

8. *Platygyrium* B.S.G.

- Platygyrium repens* (Brid.) B.S.G. On bark of trees and recently fallen logs.

Common. *Carter, Cheatham, *Cocke, *Fentress, Grainger, Knox, Sevier and Union Counties.

IX. HYLOCOMIACEAE

KEY TO GENERA

1. Paraphyllia lacking or rare 2
 1. Paraphyllia abundant 3. HYLOCOMIUM
 2. Leaf secund and rugose 1. RHYTIDIUM
 2. Leaf spreading to squarrose, often plicate but not rugose 2. RHYTIDIADELPHUS

1. *Rhytidium* (Sull.) Kindb.

Rhytidium rugosum (Hedw.) Kindb. On exposed ledges near the summit of Roan Mt. Rare. Carter County.

2. *Rhytidiadelphus* (Lindb.) Warnst.

KEY TO SPECIES

1. Leaf smooth beneath, slenderly acuminate 1. *squarrosus*
 1. Leaf spinose-papillose beneath, shortly acuminate 2. *triquetrus*

1. *Rhytidiadelphus squarrosus* (Hedw.) Warnst. On wet rocks in the mountains. Rare. Sevier County. This species reaches the southern limits of its known range in this area.

2. *Rhytidiadelphus triquetrus* (Hedw.) Warnst. On humus under spruce and fir. Uncommon. Carter, *Cocke, Johnson and Sevier Counties.

3. *Hylocomium* B. S. G.

KEY TO SPECIES

1. Leaf spinose-papillose beneath 1. *splendens*
 1. Leaf not spinose-papillose beneath 2
 2. Stem-leaf decurrent and coarsely dentate at base 2. *umbratum*
 2. Stem-leaf rounded-cordate at base and finely denticulate 3. *brevirostre*

1. *Hylocomium splendens* (Hedw.) B.S.G. On moist soil and rocks. Common only at high elevations. Carter, *Cocke, Johnson and Sevier Counties. Occurring in the most extensive colonies of any of our species, it may literally cover areas in the fir forests.

Variety *tenue* Sharp, described from Mt. LeConte, Sevier County, is never more than once-pinnate and resembles macroscopically *Hygrohypnum novae-caesareae*.

2. *Hylocomium umbratum* (Hedw.) B.S.G. On moist humus in the fir forests of the high mountains of eastern Tennessee. Rare. *Carter and Sevier Counties.

3. *Hylocomium brevirostre* (P.B.) B.S.G. On moist rocks and soil. Rather common in the Tennessee mountains. *Blount, *Cocke, Putnam and Sevier Counties.

X. BRYACEAE

KEY TO GENERA

1. Leaf linear-lanceolate 2
 1. Leaf ovate to lanceolate 3
 2. Leaves yellowish-green, rather shiny, compactly arranged 1. ORTHODONTIUM
 2. Leaves dark green, not shiny or compactly arranged 2. LEPTOBRYUM
 3. Leaf-cells at least four times as long as wide 3. POHLIA
 3. Leaf-cells less than four times as long as wide 4
 4. Leaves in compact rosettes 5. RHODOBRYUM
 4. Leaves not in compact rosettes 4. BRYUM

1. *Orthodontium* Schaegr.

Orthodontium pellucens (Hook.) B.S.G. On moist peat in health. Very rare. Sevier County. One of the tropical species which appear as isolated disjuncts in the Southern Appalachians.

2. *Leptobryum* Schimp.

Leptobryum pyriforme (L.) Schimp. On wet rocks and bricks. Uncommon. Blount, Knox and *Sevier Counties.

3. *Pohlia* Hedw. (*Webera* Hedw.)

KEY TO SPECIES

1. Gametophyte usually with propagula in some of the leaf-axils 4. *annotina*
1. Gametophyte without propagula 2
2. Gametophyte with a distinct metallic lustre 1. *cruda*
2. Gametophyte without such a lustre 3
3. Gametophyte of a whitish-green color, with somewhat the appearance of the genus, *Philonotis* 6. *Wahlenbergii*
3. Gametophyte of an ordinary green color 4
4. Neck as long as the rest of the capsule 2. *elongata*
4. Neck shorter than the rest of the capsule 5
5. Capsule about twice as long as wide 3. *nulans*
5. Capsule often as wide as long 5. *pulchella*

1. *Pohlia cruda* (L.) Lindb. On moist rocks. Uncommon. Blount, *Knox and Sevier Counties.

2. *Pohlia elongata* Hedw. On moist cliffs and banks. Uncommon. *Blount, Carter and Sevier Counties. This is restricted to elevations above 4,000 feet.

3. *Pohlia nulans* (Schreb.) Lindb. On moist soil. Not common. Blount, *Cumberland, *Grundy and Sevier Counties.

4. *Pohlia annotina* (Hedw.) Loeske. The variety *decipiens* Loeske, is found on moist sandy banks. Blount, Knox, Sevier and Unicoi Counties.

5. *Pohlia pulchella* (Hedw.) Lindb. On moist sandy bank. Rare. Sevier County.

6. *Pohlia Wahlenbergii* (W. & M.) Andrews. (*Mniobryum albicans* Limpr.) On moist soils. Common. Blount, Carter, Davidson, *Grainger, Knox, Morgan, Rutherford, Sevier and Union Counties.

4. *Bryum* Hedw.¹

KEY TO SPECIES

1. Gametophyte usually whitish or silvery; leaf without differentiated margin 7. *argenteum*
1. Gametophyte some shade of green, brown or red; leaf with at least a proximally differentiated margin 2
2. Costa long excurrent 3
2. Costa short excurrent or percurrent 4
3. Leaf-cells usually less than 1½ times as long as wide; leaf-border usually inconspicuous 5. *capillare*
3. Leaf-cells usually at least 2 times as long as wide; leaf-border usually conspicuous proximally 4. *caespitium*
4. Leaf-cells usually less than 1½ times as long as wide; border usually inconspicuous 5. *capillare*
4. Leaf-cells usually twice as long as wide; border various 5
5. Capsule purple-red at maturity, rounded at the base 6. *bicolor*
5. Capsule not unusually brilliant at maturity, tapering toward the base 6
6. Gametophytes dioicous 1. *pseudo-triquetrum*
6. Gametophytes synoicous 7
7. Leaf-border well defined 2. *binum*
7. Leaf-border inconspicuous distally 3. *intermedium*

1. *Bryum pseudo-triquetrum* (Hedw.) Schwaegr. On wet rocks. Uncommon. *Davidson, Putnam and *Sevier Counties.

2. *Bryum binum* Turn. On wet rocks. Uncommon. *Anderson, Blount, Knox and Roane Counties.

3. *Bryum intermedium* Brid. On moist soil and rocks. Uncommon. Blount, *Grainger and *Knox Counties.

4. *Bryum caespitium* Hedw. On soil and rocks. Uncommon. *Grainger and *Sevier Counties.

¹ *Bryum cyclophyllum* (Schwaegr.) B.S.G., reported from Tennessee (Sharp, 1936a), proved to be a species of *Splachnobryum*.

5. *Bryum capillare* Hedw. On ledges, rocks and tree trunks. Uncommon. Blount, Carter, Davidson, *Fentress, Knox, Sevier, Sullivan, Union and Van Buren Counties. This is a polymorphic species.

6. *Bryum bicolor* Dicks. On clay soils. Rare. Blount and *Roane Counties.

7. *Bryum argenteum* Brid. On rocks and walls. Common. *Blount, Campbell, *Carter, *Grainger, Knox, *Marion and Sevier Counties.

5. *Rhodobryum* Limpr.

Rhodobryum roseum (Weis.) Limpr. On moist soil, rocks and bases of trees. Common. Anderson, Blount, Carter, Cocke, *Grainger, *Hamilton, Knox, Marion, *Roane, Sevier and Washington Counties.

XI. MNIACEAE

Mnium Hedw.

KEY TO SPECIES

- | | |
|---|-----------------------|
| 1. Leaf without a differentiated margin | 7. <i>stellare</i> |
| 1. Leaf-margin composed of elongated cells | 2 |
| 2. Leaf-margin entire | 6. <i>punctatum</i> |
| 2. Leaf-margin toothed | 3 |
| 3. Teeth along margin in pairs | 4 |
| 3. Teeth along margin not in pairs | 5 |
| 4. Costa ending below apex, usually toothed beneath distally | 4. <i>hornum</i> |
| 4. Costa usually percurrent, not toothed beneath | 5. <i>serratum</i> |
| 5. Leaf serrate only in the upper-half or two-thirds of the leaf | 2. <i>cuspidatum</i> |
| 5. Leaf serrate to base or nearly so | 6 |
| 6. Leaf-cells collenchymatous; marginal teeth usually of 2 cells or less; operculum strongly beaked. | 3. <i>longirostre</i> |
| 6. Leaf-cells not collenchymatous; marginal teeth of 2 cells or more; operculum not beaked. | 1. <i>affine</i> |

1. *Mnium affine* Bland. On moist soil and banks. Uncommon. *Anderson, Blount, Hamilton, *Sevier and Washington Counties.

Variety *ciliare* (Grev.) C. M., a larger plant with longer marginal teeth is much more common. Grainger, Hamilton, Knox, Johnson, Sevier and Washington Counties.

Variety *rugicum* B.S.G., which resembles *M. longirostre* except for non-collenchymatous cells and almost obsolete marginal teeth, is known only from Knox county.

2. *Mnium cuspidatum* Hedw. On soil. Very common. *Anderson, Blount, Carter, *Grainger, Hamilton, Knox, *Loudon, Rutherford, *Sevier and Washington Counties.

3. *Mnium longirostre* Brid. (*M. rostratum* Schrad.) On soil. Uncommon. Anderson, Blount, *Knox, Morgan and Sevier Counties.

4. *Mnium hornum* Hedw. On siliceous ledges and soils. Common in the mountains. *Anderson, Blount, Cumberland, *Polk, *Roane and Sevier Counties. Found chiefly in the Atlantic Coastal Plain it seems to occur west of the eastern divide chiefly on the Cumberland Plateau.

5. *Mnium serratum* (Schrad.) Brid. [*M. marginatum* (Dicks.) Pal.] On moist ledges. Uncommon. Anderson, Blount, Hamilton, Knox, Sevier and Union Counties.

6. *Mnium punctatum* (Reich.) Hedw. On wet rocks. Common only at high elevations. Blount, *Carter, *Johnson, Sevier and Washington Counties.

Variety *clatum* Schimp., characterized by its huge size and shorter costa, has been found in Johnson and Sevier Counties. In view of some of Wettstein's (1932) work, it is probable that this variety arose by a doubling of the chromosome-number.

7. *Mnium stellare* (Reich.) Hedw. On moist bluffs and bases of trees. Blount, Knox, Putnam and Sevier Counties.

XII. AULACOMNIACEAE

Aulacomnium Schwaegr.

KEY TO SPECIES

- | | |
|--|-------------------------|
| 1. Leaf-apex broad, strongly serrate | 1. <i>heterostichum</i> |
| 1. Leaf-apex acute, serrulate to serrate | 2 |

2. Basal cells of leaf not swollen; propagula fusiform 2. *androgynum*
 2. Basal cells of leaf swollen; propagula flattened 3. *palustre*

1. *Aulacomnium heterostichum* (Hedw.) B.S.G. On moist banks and bases of trees. Very common. Blount, Cheatham, Cocke, Davidson, *Fentress, Grainger, Hamilton, *Johnson, Knox, Lincoln, *Morgan, *Polk, Roane, Sevier and Washington counties.

2. *Aulacomnium androgynum* Schwaegr. has been reported from Tennessee by Sullivant (1856). But the Chimney Rocks are probably in North Carolina and not in Tennessee. The writer has seen no material collected in Tennessee.

3. *Aulacomnium palustre* Schwaegr. Wet soil and bogs. Common. *Blount, *Carter, Campbell, *Cumberland, Fentress, Hamilton, Johnson, *Knox, Marion, Morgan, Polk, Rhea, *Sevier, *Unicoi and Wilson Counties.

XIII. BARTRAMIACEAE

KEY TO GENERA

1. Leaf lanceolate to linear-lanceolate 1. BARTRAMIA
 1. Leaf shorter, ovate-lanceolate 2. PHILONOTIS

1. *Bartramia* Hedw.

Bartramia pomiformis Hedw. On moist banks and ledges. Common. Blount, Cheatham, Cocke, *Davidson, Grainger, Hamilton, Knox, *Morgan, *Roane, Sevier and Washington Counties.

2. *Philonotis* Brid.

KEY TO SPECIES

1. Perigonia gemmiform, often appearing lateral 1. *longiseta*
 1. Perigonia discoid, terminal 2
 2. Leaf-cells papillose only at the upper ends 3
 2. Leaf-cells papillose at the lower ends, rarely at the upper or both ends 4
 3. Leaf-cells linear; leaves triangular-lanceolate to ovate-lanceolate 2. *marctica*
 3. Leaf-cells oblong to oblong-linear, broader; leaves ovate-lanceolate 3. *Muhlenbergii*
 4. Leaf-margin plane or recurved only at the base, singly serrate 4. *caespitosa*
 4. Leaf-margin revolute and doubly serrate 5. *fontana*

1. *Philonotis longiseta* (Rich.) E. G. Britt. On moist bluffs and banks. Uncommon. Blount, *Cocke, *Davidson, Knox, Marion, Morgan, Putnam and *Sevier Counties.

Forma *propagulicaulis* Flowers, is known from Blount County.

Forma *polygama* Flowers, was originally collected in Campbell County.

2. *Philonotis marctica* (Willd.) Brid. Moist soil. Rare. Anderson County.

3. *Philonotis Muhlenbergii* (Schwaegr.) Brid. Wet rocks. Not common. Fentress and Sevier Counties.

4. *Philonotis caespitosa* Wils.

Variety *adpressa* Dism., has been found on wet rocks in Carter County.

Variety *laxa* (Warnst.) Loeske & Warnst., has been found in Sevier County.

5. *Philonotis fontana* Brid. On wet rocks. Not very common. Blount, Roane, Sevier and Unicoi Counties.

Order VI. SPLACHNALES

KEY TO FAMILIES

1. Total length of gametophyte with attached sporophyte less than 1 mm. I. EPHEMERACEAE
 1. Gametophyte alone usually much more than 2 mm. high 2
 2. Gametophyte growing on ashes, soil, rocks or bricks II. FUNARIACEAE
 2. Gametophyte growing on dung III. SPLACHNACEAE

I. EPHEMERACEAE

KEY TO GENERA

1. Capsule with rudimentary operculum; capsule-wall a single layer of cells in thickness 1. NANOMITRIUM
 1. Capsule without operculum; capsule-wall two layers of cells in thickness 2. EPHEMERUM

1. *Nanomitrium* Lindb.

KEY TO SPECIES

1. Leaf serrulate; calyptra central 1. *Austinii*
 1. Leaf entire; calyptra often eccentric 2. *synoicum*
 1. *Nanomitrium Austinii* (Sull.) Lindb. On mucky soil. Rare. Fentress and Johnson Counties.
 2. *Nanomitrium synoicum* (James.) Lindb. On mucky soil. Very rare. *Johnson County.

2. *Ephemerum* Hampe

KEY TO SPECIES

1. Leaf ecostate 1. *serratum*
 1. Leaf costate 2
 2. Leaf narrow, often linear, with a coarsely spinose, apical hair 3. *spinulosum*
 2. Leaf broader at the base; leaf-apex toothed but not noticeably spinose 2. *crassinervium*

1. *Ephemerum serratum* (Hedw.) Hampe. Only variety *minutissimum* (Lindb.) Grout, is known from Tennessee. On sandy soils. Uncommon. Fentress and Knox Counties.

2. *Ephemerum crassinervium* (Schwaegr.) C. Muell. Only variety *papillosum* (Aust.) R. & C. is known from Tennessee. On sandy soils. Rare. Fentress County.

3. *Ephemerum spinulosum* Schimp. On sandy soil. Rare. Fentress County.

Variety *hystrix* (Lindb.) Grout is known from Cumberland County.

Species of this genus and family are probably over-looked because of their small size.

II. FUNARIACEAE

KEY TO GENERA

1. Capsule immersed 1. *APHANORRHEGMA*
 1. Capsule exserted 2
 2. Capsule symmetrical, urn-shaped 2. *PHYSCOMITRIUM*
 2. Capsule asymmetrical, elongated 3. *FUNARIA*

1. *Aphanorrhagma* Sull.

Aphanorrhagma serratum (Hook. & Wils.) Sull. On alluvial soil. Not common. *Claiborne and *Johnson Counties.

2. *Physcomitrium* Brid.

Physcomitrium turbidum (Mx.) Brid. On moist soils. Very common. *Anderson, Blount, Davidson, *Grainger, Hamilton, Knox, Putnam and Sevier Counties.

3. *Funaria* Hedw.

KEY TO SPECIES

1. Costa frequently excurrent; spores 20-30 microns in diameter 1. *flavicans*
 1. Costa infrequently excurrent; spores 12-15 microns in diameter 2. *hygrometrica*

1. *Funaria flavicans* Mx. On calcareous soils. Not common. Blount, Davidson, Knox and *Marion Counties.

2. *Funaria hygrometrica* Hedw. On ashes and calcareous soils. Common. Anderson, Bledsoe, Blount, *Grainger, Hamilton, Knox and Sevier Counties.

Variety *calvescens* B.S.G., is known from Mt. LeConte in Sevier County.

III. SPLACHNACEAE 1

Tetraplodon B.S.G.

Tetraplodon pennsylvanicus (Brid.) Sayre. On dung in bogs. Very rare. Johnson County. This species is more common in the coastal plain.

1 A species of *Splachnobryum* has been found on the walls of a greenhouse (now razed) in Knox County.

Order VII. POLYTRICHALES

KEY TO FAMILIES

1. Gametophyte often with a cluster of terminal gemmae surrounded by a leafy cup; peristome of 4 teeth.....I. TETRAPHIDACEAE
1. Gametophyte without gemmae; peristome of 16 or more teeth 2
2. Gametophyte usually large (except *Pogonatum*); leaf with lamellae; capsule exerted on long setaII. POLYTRICHACEAE
2. Gametophyte less than 1 cm. high; leaf without lamellae; capsule immersedIII. DIPHYSCIACEAE

I. TETRAPHIDACEAE

Tetraphis Hedw.

Tetraphis pellucida Hedw. [*Georgia pellucida* (L.) Rabenh.] On logs and occasionally on rocks. Rather common in the mountains. Anderson, *Blount, *Grainger, Johnson, Marion and Sevier Counties.

II. POLYTRICHACEAE

KEY TO GENERA

1. Calyptra not densely hairy; capsule cylindrical1. ATRICHUM
1. Calyptra densely hairy; capsule angular or cylindrical 2
2. Capsule cylindrical; gametophyte small, less than 1/2 cm. high2. POGONATUM
2. Capsule usually angular; gametophyte large3. POLYTRICHUM

1. *Atrichum* Beauv. (*Catharinaca* Ehrh.)

KEY TO SPECIES

1. Leaf ovate-elliptical or obovate; lamellae small1. *crispum*
1. Leaf lanceolate to lingulate; lamellae very conspicuous 2
2. Costa and lamellae narrower than one-fifth the width of the leaf at the middle2. *undulatum*
2. Costa and lamellae one-fourth to two-thirds the width of the leaf at the middle3. *angustatum*

1. *Atrichum crispum* (James) Sull. In springs, edges of brooks and moist soil in the mountains. Not common. Carter, Johnson, Putnam and Sevier Counties. This species is more frequent in the eastern coastal plain than elsewhere.

Variety *molle* (Holz.) Frye, found once in Hamilton County, is characterized by higher lamellae and the teeth on the back of the costa.

2. *Atrichum undulatum* (Hedw.) Beauv. On moist, acid, clay soils. Common. *Blount, *Grainger, *Knox, Morgan, Sevier and Union Counties. A form in wet habitats in the mountains resembles *A. undulatum* except being more than twice as large and probably having double the number of chromosomes characteristic of the common form (cf. Wettstein, 1932).

3. *Atrichum angustatum* (Brid.) B.S.G. On dry acid soils. Common. *Anderson, Blount, Campbell, Cheatham, *Cocke, Davidson, Grainger, Hamilton, Knox, *Polk, Sevier, Union and Washington Counties.

2. *Pogonatum* Beauv.

Pogonatum pennsylvanicum (Hedw.) Paris. [*P. brevicaulis* (Brid.) Beauv.] Moist clay banks in the mountains. Relatively common. *Blount, Carter, Morgan, *Roane and Sevier Counties. This moss forms large mats of persistent protonemata which seem to be important in checking erosion of recently exposed banks.

3. *Polytrichum* Hedw.

KEY TO SPECIES

1. Leaf-apex not piliferous; margin not involute 2
1. Leaf-apex piliferous; margin involute 5
2. Capsule not over 1 1/2 times as long as wide; marginal cells of lamellae almost reniform in cross-section4. *commune*
2. Capsule at least 2 times as long as wide; marginal cells of lamellae otherwise.... 3

3. Marginal cells of lamellae in cross-section seldom if ever flattened at the top 1. *formosum*
 3. Marginal cells of lamellae in cross-section flattened or concave at the top 4
 4. Marginal cells of lamellae with smaller cavities and thicker walls than the other cells 2. *ohioense*
 4. Marginal cells of lamellae similar to the other cells 5. *decipiens*
 5. Apical leaf-hair reddish-brown throughout 5. *juniperinum*
 5. Apical leaf-hair whitish throughout or occasionally reddish-brown at the base only 6. *piliferum*

1. *Polytrichum formosum* Hedw. (*P. attenuatum* Menz.). On exposed siliceous rocks. Not common. Sevier County.

2. *Polytrichum ohioense* R. & C. On relatively acid soils. Common. Anderson, Blount, Carter, Cheatham, Cocke, Grainger, Hamilton, *Knox, *Polk, *Roane, *Scott, Sevier and *Washington Counties.

3. *Polytrichum decipiens* Limpr. Moist soil. Rare. Found only on Thunderhead Mt., Blount County. As Nichols (1937) has pointed out, this is hardly distinct from *P. ohioense*.

4. *Polytrichum commune* (L.) Hedw. Moist acid soil. Not very common. *Blount, *Carter, *Fentress, Johnson, *Roane and Sevier Counties.

5. *Polytrichum juniperinum* (Willd.) Hedw. Moist acid soils. Not very common. Blount, Campbell, Carter, Johnson, Marion, Putnam and Sevier Counties.

6. *Polytrichum piliferum* (Schreb.) Hedw. Rocky and sandy soils. Rare. Known only from Gregorys Bald, Blount County.

III. DIPHYSCIACEAE

Diphyscium Mohr

Diphyscium sessile (Schmid.) Lindb. [*Webera sessilis* (Schmid.) Lindb.] On exposed peaty soils, occasionally on bluffs. Common. *Anderson, Blount, Cheatham, *Grainger, Hamilton, *Hancock, *Morgan and Sevier Counties.

Class V. ANTHOCEROTAE

Only one order, *Anthocerotales*, and one family, *Anthocerotaceae*, in the class.

ANTHOCEROTACEAE

KEY TO GENERA

1. Sporophyte more than 10 mm. in length, with stomata 1. ANTHOCEROS
 1. Sporophyte less than 5 mm. in length, without stomata 2. NOTOTHYLAS

1. *Anthoceros* L.

KEY TO SPECIES

1. Spores black 2. *crispulus*
 1. Spores yellow 2
 2. Thallus forming a boot-like involucre over 2 mm. high around the base of the sporophyte 1. *carolinianus*
 2. Involucre less than 2 mm. high 3. *laevis*

1. *Anthoceros carolinianus* Michx. On wet banks. Rare. *Blount and Sevier Counties.

2. *Anthoceros crispulus* (Mort.) Douin. On wet soil. Rare. Knox and *Sevier Counties.

3. *Anthoceros laevis* L. On wet soil and banks. Rather common. *Carter, Marion, *Polk and Sevier Counties.

Howe (1896) reported *A. punctatus* L. from Tennessee without reference to locality.

2. *Notothylas* Sull.

Notothylas orbicularis (Schwein.) Sull. On moist alluvial soils. Not common. *Claiborne, Cumberland and *Johnson Counties.

C. BRYOPHYTES NEW TO SCIENCE AND RANGE-EXTENSIONS
DISCOVERED DURING THESE INVESTIGATIONS

No new species or varieties are described in this paper. However, during the course of these investigations, nine new species, one new variety, and one new form were found. Of the new species seven are known from Tennessee; the other two, *Schlotheimia lancifolia* and *Bartramidula carolinae*, were collected in southwestern North Carolina less than 40 miles from the Tennessee border. The latter will probably be collected also in Tennessee.

Of the plants previously unknown to science, descriptions of all but two species have been published. *Homalia Sharpii* was described by Williams (1931) and *Schlotheimia lancifolia* by Bartram (1932). *Forma polygama*, of *Philonotis longiseta* was mentioned first in the monograph by Flowers (1935). Evans (1938) described recently *Cololejeunea ornata* and the writer described the following: *Tortula propagulosa*, *Fabronia imperfecta* and *Hylocomium splendens* var. *tenuis* (Sharp, 1933), *Acrobolbus rhizophyllus* (Sharp, 1936b), and *Bartramidula carolinae* (Sharp, 1936a). Of the remaining two, a *Plagiochila* species is being described by Dr. H. L. Blomquist, Duke University, and a new *Ditrichum* is being studied by Mr. R. T. Wareham, Ohio State University.

Some extensions of the known range of bryophytes have either been published (Sharp 1936a, 1938a) or are recorded here. Especially interesting are the first reports of the occurrence of *Riccardia incurvata* and *Plagiochila tridenticulata* in North America north of Mexico. Further important extensions of known distributions have been noted for such species as *Crossotolejeunea bermudiana*, *Rectolejeunea Maxonii* and *Homalothecium Bonplandii*. Less striking but interesting extensions in the known range are given for many species such as *Nardia scalaris*, *Cephaloziella spinicaulis*, *Sphagnum Pylaesii*, *Dicranum rugosum* and *Myurella julacea*.

D. SUMMARY

The bryophytes collected in eastern Tennessee during these investigations comprise five classes, fourteen orders, fifty-six families, one hundred and seventy-three genera, four hundred and twenty-six species, including six represented only by varieties, twenty-six varieties, including those just mentioned, and two forms. Of those seven species, one variety and one form were previously unknown to science. Extensions in known range are noted for a large number of species. A few genera and species are reported here for the first time from North America north of Mexico. Lesser extensions in a southerly direction are recorded for many other species.

3. Ecologic Studies

A. INTRODUCTION

The area under investigation includes about 27,000 square miles, embracing sixty-five counties, of the eastern portion of Tennessee, extending westward to include Robertson, Creatham, Williamson, Maury and Giles Counties.

This region includes portions of four physiographic provinces as outlined by Fenneman (1938). They are, east to west, (1) the Blue Ridge, (2) Ridge and Valley, (3) Appalachian Plateaus and (4) the Interior Low Plateau (see Fig. 1).

The portion of the Blue Ridge Province lying in eastern Tennessee is a narrow band occupying a part of the eastern row of counties; its terrain is extremely rugged. The highest point is Clingman's Dome (6,642 feet) in the Great Smoky Mountains and the lowest, on the Little Tennessee River, is slightly less than 800 feet. Probably more than a hundred peaks above 5,000 feet occur here. The rocks are nearly all non-calcareous, with the exception of those in a few coves such as Cades Cove in the Great Smoky Mountains. The Blue Ridge drops off abruptly to the Ridge and Valley Province on the west.

The Ridge and Valley Province in Tennessee consists of the valleys of the Tennessee River and its tributaries with intervening ridges. The lowest point is approximately 650 feet near Chattanooga; the highest, more than 2,500 feet on the summit of Clinch Mountain. The rocks are mainly calcareous (limestones, marbles and dolomites), with some shale and sandstone, the latter capping many of the ridges.

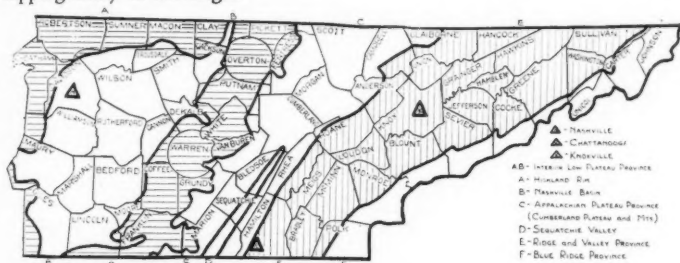


Fig. 1. County map of eastern Tennessee with the general outline of physiographic regions.

The Appalachian Plateau Province is represented in Tennessee by the Cumberland Plateau and Mountains which rise abruptly to the west of the Ridge and Valley Province. It exhibits an average elevation of approximately 2,000 feet, except in the northeast where the Cumberland Mountains rise to a height above 3,500 feet. The rocks are siliceous (sandstones and conglomerates). The Sequatchie Valley which penetrates the Cumberland Plateau to the south is in most respects similar to the Ridge and Valley Province.

The remainder of the area involved in this investigation lies in the Interior Low Plateau Province. This Province may be subdivided into the Highland Rim and the Nashville Basin. The rocks in both are mainly limestone. The Basin varies from 500 to 700 feet, and is surrounded by the Rim, the average elevation of which is about 1,000 feet.

The climate of eastern Tennessee is much affected by the elevation. This fact is reflected in the precipitation and temperature averages. The lowest

mean annual precipitation (45-50 inches) occurs in the upper portion of the Tennessee Valley. The other extreme is found at high elevations in the Great Smoky Mountains where the annual average may be in excess of 80 inches. The remainder of eastern Tennessee has a mean annual precipitation of 45 to 55 inches with the exception of a portion of the Cumberland Plateau where it varies from 55 to 60 inches.

The large average number of rainy days is also important in the growth of bryophytes. This number is particularly high in the mountains where fogs and clouds increase the humidity still further. Precipitation is relatively well distributed throughout the year over the entire area studied.

The distribution of mean annual temperature contours can be correlated in part with the topography. The extremes in temperature to be found in the area are -30°F. and 106°F. , the former in the high mountains, the latter in the Nashville Basin. For a general summary of natural conditions in the Tennessee Valley, the reader should see Hudson, et al. (1936).

The natural vegetation of eastern Tennessee represents a part of three Formations. Isolated areas above 4,500 feet in the Blue Ridge Province exhibit spruce-fir forests which belong to the Northern Coniferous Forest Formation. Some of the stands have been described by Cain (1935). Valleys and north-facing slopes at elevations between 3,000 and 5,000 feet are frequently covered with forests similar to those of the Eastern Hemlock Region¹ described by Nichols (1935). The remainder of the Blue Ridge Province in Tennessee is an intricate mosaic of forest types of the Deciduous Forest Formation. Dry ridges and exposed southern slopes may have an edaphic climax of table mountain, pitch, and scrub pine. The best virgin timber in the eastern United States from the standpoint of size and number of species is to be found in this Province.

The Ridge and Valley Province was originally covered chiefly by deciduous forest types. Except for the ridges, the land is being utilized mainly for agricultural purposes. The ridges exhibit oak-pine and pine forests of a successional or edaphic climax nature.

The Cumberland Plateau and Mountains are covered mainly with pine-oak forests on the dry sites and oak-pine forest on the moister sites; on the wet sites oak grows mixed with red maple and sour gum. Hickories were probably a more prominent part of the vegetation in the past than they are today. In the gorges and deep valleys are outliers of the Forest Formation described by Nichols (1935).

The Interior Low Plateau was formerly forested chiefly by oak-hickory with stands of red cedar (cedar barrens) on the poorer and drier portions. Much of this Province now consists of farms with the remaining forests limited to the ridges and thin soils.

It is interesting to note that eastern Tennessee does not and probably never did produce extensive stands of the Beech-Maple climax. The condi-

¹ Some ecologists refer to this region as the Hemlock-Hardwood Region.

tions of the present day forests in a large portion of this area are depicted in generalized form in the report of Hudson et al. (1936).

Due to its great diversity of microclimates as a result of differences in elevation and direction of slope, its varied rocks, its great number of ligneous species which may serve as substrata, and its relatively high precipitation and humidity, eastern Tennessee is an area extremely favorable to the growth of a luxuriant and diverse bryophytic flora.

B. HABITATS AND FACTORS

Actual experimental data concerning environmental factors in relation to bryophytes are meager (Cf. Davy de Virville, 1927). There are two primary reasons for this situation: firstly, bryophytes are not considered to be of much economic importance and consequently have been little studied; secondly, they can be grown on artificial media in the laboratory with only mediocre success, and failure has attended most attempts to grow them on natural substrata under experimental conditions. On this point, Garjeanne (1932) says: "Though it is sometimes possible to grow them for a shorter or longer period, in the end they always die: this is certainly a great handicap to gaining a more intimate knowledge of the Bryophytes."

In the absence of convincing experimental data, specific field and laboratory observations have been made, and from these empiricisms certain generalizations may be drawn. In fact, bryophytes exhibit so many physiological and ecological characteristics in common with the vascular plants that we may assume with some degree of assurance that the former will not only be affected by the same factors as the latter, but also in much the same manner. The discussions of Garjeanne (1932) and Richards (1932) encourage this assumption.

Moisture conditions of both the substratum and the atmosphere are of prime importance in the growth and survival of bryophytes. The large number of bryophytic species in eastern Tennessee can be primarily correlated with the relatively high humidity, particularly of the mountain section where favorable moisture conditions are maintained by the high annual precipitation, large number of cloudy days, drizzly rains and frequent fogs. Water dripping from trees as a result of fog-condensation is of importance in the higher Appalachians as it is on the west coast of the United States. It should be emphasized that many mountain ravines do not become dry in the worst drouths.

Effects which seem superficially to be controlled by light and temperature may actually be the result of moisture conditions modified by those two factors. The higher incidence of bryophytes on certain sides of trees and on north-facing slopes and banks is usually ascribable to the favorable moisture conditions rather than the lower light intensities and depressed temperatures (cf. Martin, 1938). The disappearance of the *Hylocomium* ground-cover from the spruce and fir forests wherever trees are cut or blown down is undoubtedly due in large part to the changed conditions of moisture.

Because of the abundance of moisture in eastern Tennessee, restriction of

certain bryophytes to particular habitats is not as rigid as in drier areas. The abundant moisture evidently compensates in part for deficiencies in other factors. *Leptodon trichomitrium*, *Drummondia prorepens* and *Leucodon julaceus* grow usually on bark but may be found occasionally on rocks. *Hedwigia ciliata* ordinarily occurs on siliceous rocks but has been found on the bark of an oak. Certain mosses have been collected on the giant lichen, *Gyrophora Dillenii*, (Sharp, 1930), and subsequently liverworts have been noted on the same type of substratum. These facts, however, do not invalidate the generalization that some bryophytes may serve as indicators of certain habitats as suggested by Welch (1935) and others.

The bryophytes on the butts of trees (particularly beech) in the gaps of the high mountains show great similarity (cf. Cain & Sharp, 1938) to those species of the top-limb flora below those gaps. This similarity may be correlated with the fogs (clouds) so common in these areas. They roll through the gaps almost at ground level and become progressively higher in the trees toward the base of the mountains.

The actual water requirements of bryophytes vary with the species: some grow directly in the water; others, on exposed and dry rock. Relationships between the structure of mosses and the absorption and retention of water have been pointed out by Roberts and Haring (1937). Anderson and Beaven (1937), and Cain and Penfound (1938) have discussed the usual moisture conditions of the habitats for certain bryophytes. Billings and Drew (1938) studied the moisture conditions of the bark beneath certain bryophytic communities in eastern Tennessee. Ochsner (1927) suggests that some bryophytes may be used alone or in conjunction with vascular plants as quantitative indicators of moisture conditions.

Only one of our species, *Ricciocarpus natans*, is aquatic and unattached. *Riccia fluitans*, which may occur floating, has been found in eastern Tennessee only on mud. Those that grow submerged but attached are: *Rhacomitrium aciculare*, species of *Fontinalis*, *Dichelyma capillaceum*, *Leptodictyum riparium*, *Fissidens julianus* and *F. grandifrons*.

In sharp contrast, *Hedwigia ciliata*, *Ptychomitrium incurvum*, *Grimmia apocarpa* and *Orthotrichum strangulatum* may be found on very dry rocks. Most of our bryophytes display water requirements between these extremes.

Light as a single factor is difficult to evaluate because of its effect on temperature and indirectly on humidity. One generalization, however, may be made: light requirements of bryophytes are not generally high. This situation is emphasized by the occurrence, in eastern Tennessee, of many of our bryophytes in densely shaded habitats (the fir forest, north-facing slopes and cliffs, dark crevices and rocks beneath overhanging cliffs); the most extensive bryophytic communities (*Hylocomium*) are found on the poorly illuminated floor of the spruce-fir forest. The present observations afford little data relative to the light tolerance, *per se*, of bryophytes.

Difficulty also attends the evaluation of the temperature factor because of its effects on humidity. Hesselbo (1913) has shown that aquatic mosses in

Iceland may grow at temperatures of approximately 40°C. Some of our rock-growing mosses, such as *Hedwigia ciliata*, must withstand temperatures in excess of 45 or 50°C. In contrast, temperatures as low as -34°C. in the Great Smoky Mountains of eastern Tennessee seem to have little or no effect upon the survival and subsequent growth of bryophytes.

Probably no substratal factor has been more thoroughly investigated than that of hydrogen-ion concentration. Observations have been made concerning a relatively large number of bryophytes by Robinove and La Rue (1928), Montgomery (1931), Apinis and Diogues (1933), Apinis and Lacis (1934-35) and Ikenberry (1936). Their findings indicate that many bryophytes are restricted by pH. It follows that those bryophytes with narrow limits may serve as pH indicators. In eastern Tennessee, as elsewhere, species of the family, Polytrichaceae, and the genera, *Dicranum*, *Hypnum* (*sensu lato*) and *Leucobryum* are as characteristic of acid substrata as are many of the vascular plants such as the Ericales. Circumneutral substrata may be indicated by *Weisia controversa*, *Physcomitrium turbinatum*, *Funaria flavicans* and species of *Anomodon*. Many of our species such as *Ceratodon purpureus* may grow vigorously on substrata with a very wide range of pH.

Bryophytes may indicate the pH of various barks and rocks. The analyses of certain bryophytic communities by Cain and Sharp (1938) would indicate that coniferous bark is more acid than that of deciduous trees; this conclusion has subsequently been substantiated by Billings and Drew (1938). Communities on conifers are dominated by species of *Hypnum* (*sensu lato*) and *Hylocomium*, bryophytes which usually grow on acid substrata. Those on many deciduous trees such as *Liriodendron* and *Acer* are dominated by species of *Anomodon*, *Leucodon*, *Ulota*, *Neckera* and *Leptodon*, bryophytes which are more frequently found on substrata with a higher pH than that of coniferous bark. It is possible that some of these differences may be accounted for on a basis of moisture conditions rather than pH.

The effect of soot and smoke on the pH of tree-bark in the cities needs investigation, for *Tortula pagorum* in eastern United States seems limited to trees near habitation.

The qualitative change in communities during the decortication of fallen deciduous trees indicates that their decaying wood is more acid than their bark. The bryophytes enumerated above as occurring on their bark are replaced following decortication by *Tetraphis pellucida* and species of the *Hypnum* complex.

The difference in pH of siliceous and calcareous rocks is well known. In addition to many of the species mentioned by Nichols (1916), it should be noted that *Hedwigia ciliata*, *Hylocomium brevirostre*, *Tetraphis pellucida* and species of the *Hypnum* complex are common on siliceous substrata in our area. Incidentally, the *Hedwigia* found on bark was found on that of an oak, which is acid in reaction. Calcareous substrata are inhabited by *Grimmia apocarpa*, *Orthotrichum strangulatum*, *Hymenostylium recurvirostrum* and other species with similar requirements. Aside from pH little is known about the chemical effects of the substratum.

The only physical condition of the substratum so far discussed is that of moisture. In addition porosity affects the ease of attachment of bryophytes. Another important factor is the regularity with which the bark scales off or rock-surfaces disintegrate. One reason for the scarcity of bryophytes on some of our trees such as *Picea*, *Halesia* and *Platanus* is the continuous exfoliation of the bark. Soft sandstones often disintegrate rapidly enough to prevent the extensive growth of bryophytic communities.

No single factor accounts for all the differences between the bryophytes found in diverse habitats. It is the interaction of factors which ultimately determines the nature of the habitat and its flora. Bryophytes, in part because of their size, are much more responsible to microclimates than are vascular plants. Eastern Tennessee with its variations in temperature and precipitation due to the mountains, and in kinds of substrata due to variety of rocks and ligneous flora, includes a large number of heterogeneous habitats. This fact partially explains the large number of bryophytes found in this region.

The only relatively uniform habitat, as indicated by bryophytic communities, which is extensive in eastern Tennessee is the floor of the spruce-fir forest which is found on the tops of our higher mountains; this floor is often covered with a mat of *Hylacomium splendens* acres in extent. Other communities occupy smaller areas, the largest of which is but a few square feet or yards.

Bryophytes themselves may modify their habitats directly or indirectly. This fact has been noted by Kurz (1928), Cain and Penfound (1938), and others. In eastern Tennessee their most important action is the retention of moisture, which accelerates the decortication and decay of fallen trees and the disintegration of rocks. It should be noted that, by the combined effects of water and carbon dioxide from bryophytes, calcareous rocks are etched. *Didymodon tophaceus*, *Eucladium verticillatum* and *Hymenostylium recurvirostrum* may precipitate calcium carbonate from water, and thus form the tufa which may be noted in small quantities on certain cliffs and about calcareous springs in eastern Tennessee. Mosses in the role of tufa-formers have been discussed by Emig (1918), Taylor (1919) and Daubenmire (1928). At Alum Cave in Sevier County there seems to be some relationship between the growth of *Merceya lingulata* and the formation of small quantities of limonite. In general these modifications are brought about rather slowly.

Attempts have been made both abroad (Cajander, 1909, 1926) and in North America (Brinkman, 1929; Heimburger, 1933, and Ilvessalo, 1929) to use bryophytes in the evaluation of sites. Their use seems justified as they may indicate finer differences than the larger plants. Olsen (1917) found that certain epiphytic mosses might be correlated with sandy or calcareous soils. However, care must be exercised that the intimate relationship of the bryophytes to the surrounding vegetation is not ignored and the worth of the evaluation thereby decreased. In eastern Tennessee it seems more profitable at the present time to study bryophytes in relation to other vegetation rather than to site evaluation.

C. INVASION AND SUCCESSION

Invasion must occur before succession may begin. Literature dealing with invasion by bryophytes is meager, and most of it in this country is relatively recent. Skutch (1929) noted the invasion of *Marchantia polymorpha* following fires. Torrey (1932a, 1932b) and Graff (1935, 1936) discuss the same phenomenon. Such invasions were noted in Johnson County, Tennessee, in the spring and early summer of 1934. In that portion of Shady Valley bog which had been burned over the previous summer, large areas were covered by *Marchantia polymorpha* with which *Pleuroidium palustre* was associated. Wood ashes in eastern Tennessee are frequently colonized by *Funaria hygrometrica* and *Barbula convoluta*.

Griggs (1933, 1935) has recorded the colonization of the Katmai ash by two liverworts. It is worthy of note that both of these, *Lophozia bicrenata* and *Cephaloziella byssacea*, occur in eastern Tennessee where the former is frequently found on denuded clay. The *Lophozia* has at times been accompanied by a *Cephaloziella* which is probably the same species mentioned by Griggs but it lacked sufficient diagnostic characters to be identified with certainty.

Banks in the mountains which have been denuded by landslides, road- or trail-building are readily colonized by extensive mats of *Pogonatum pennsylvanicum*. The gametophytes of this species consist largely of a felt-like mat of protonemata, which seems to be important in checking sheet erosion. The role of certain mosses in erosion has been pointed out by Conard (1935). On banks which are very moist, the *Pogonatum* is associated with *Nardia crenulata*, *Dicranella varia* and *Ditrichum pusillum*. On wet banks *Conocephalum conicum* and often *Pellia epiphylla* occur alone or in company with the above mentioned species. All of these in a few years are succeeded by herbs except on the very steepest exposures. There the felt-like mats may peel off every year or two, particularly after freezing. Observations lead one to believe that erosion, even under these conditions, would be more rapid without the bryophytes, since these mats continually renew themselves.

The edge of the soil overlying road or traidside banks is usually colonized by *Ditrichum pallidum* or a mixture of *Diphyscium sessile* and species of *Cladonia* and other lichens.

Bryophytes are active in the revegetation of abandoned fields in the Tennessee Valley. During the first year that a field has lain fallow *Physcomitrium turbinatum*, *Weisia controversa* and *Astomum Sullivantii* are common invaders. Less frequently *Phascum cuspidatum* var. *piliferum*, *Sphaerocarpos texanus* and species of *Pleuroidium* and *Bruchia* may be found. Ruderals are scarce the first year but as their numbers increase, the relative abundance of the bryophytes decreases.

As indicated elsewhere, the bryophytes which are found on flood plains in Tennessee and may even precede the phanerogams are: *Riccia fluitans*,

Notothylas orbicularis, *Aphanorrhegma serratum* and species of *Ephemerum* and *Nanomitrium*.

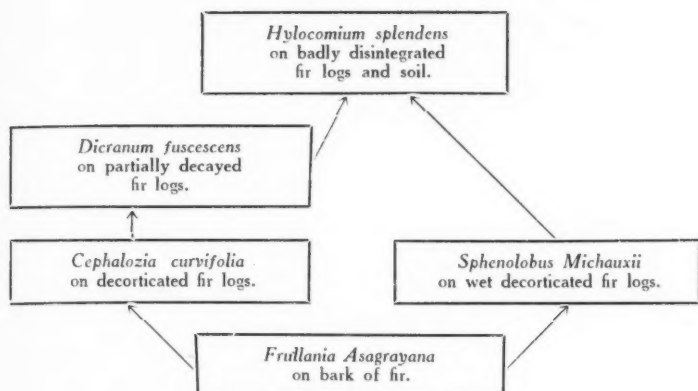
Rocks are generally very slowly colonized by bryophytes. On certain cliffs in eastern Tennessee, areas denuded of bryophytes have shown little decrease in size in five years. That rocks will be colonized in time is attested by the fact that many boulders, cliffs and bluffs are essentially covered with bryophytes. There, with or without the assistance of lichens, they accelerate the rate of accumulation of humus; with sufficient humus, herbs will succeed the bryophytes. During the earlier stages of humus-accumulation on many rocks in eastern Tennessee, lichens may succeed bryophytes or the reverse may occur. Occasionally both types of succession may take place on the same surface. The details of these successions demand the attention of a lichenologist.

The invasion of certain bluffs in our area is similar in many ways to that described by Oosting and Anderson (1937). Dry siliceous rocks support as pioneers: *Hedwigia albicans*, *Ptychomitrium incurvum* and species of *Grimmia*. On more moist situations, *Hylocomium brevirostre*, *Thuidium delicatulum*, *Dicranum fulvum*, *Oncophorus Raui*, *Anomodon attenuatus* and species of *Metzgeria*, *Plagiochila*, *Dicrandodontium*, *Plagiothecium* and of the family, *Lejeuneaceae* may appear. The pioneers on wet, siliceous rocks include *Racomitrium aciculare*, *Porotrichum alleghaniense*, species of *Marsupella*, *Scapania*, *Andreaea*, *Sematophyllum* and *Hygrohypnum*.

Dry calcareous rocks are invaded by *Orthotrichum strangulatum*, *Grimmia apocarpa* and species of *Tortula*. With more moisture *Radula andicola*, *Neckera complanata*, species of *Anomodon* and *Brachythecium* and occasionally *Leptodon trichomitrium*, *Homalia Sharpii* and species of the family *Lejeuneaceae* may develop. On wet calcareous rocks the common bryophytic invaders are: *Hymenostylium recurvirostrum*, *Hyophila Tortula*, *Fissidens grandifrons*, and species of *Amblystegium* (*sensu lato*).

Crevice of bluffs or cliffs are colonized by bryophytes different from those invading the surfaces of rocks. Most crevices usually have accumulated some humus and the species found there are often similar to those on soil. The first bryophytes to appear in the crevices of calcareous rocks include *Barbula unguiculata*, *Tortella humilis*, *Weisia controversa*, *Gymnostomum calcareum*, and species of *Fissidens* and *Leskea*. Crevices of siliceous rocks are colonized by *Trichostomum tenuirostre*, *Gymnostomum rupestre*, *Rhabdoweisia denticulata*, *Diphyscium sessile*, *Leucobryum glaucum* and many other species.

Relatively little has been published in this country in relation to the ecologic succession of bryophytes. The paper by Cooper (1912) was among the earliest. It has been followed by few others, notably those of Taylor (1920a), Cain and Penfound (1938), Billings and Drew (1938) and Cain and Sharp (1938). The last-mentioned points out some of the successions which may be encountered in the fir forests in eastern Tennessee. These successions in terms of the dominant species may be represented by the following diagram.



In the hardwoods at lower elevations in the Great Smoky Mountains, the corticolous bryophytes, *Anomodon attenuatus*, *A. rostratus*, *A. Rugelii*, *Leucodon brachypus*, *Neckera pennata* and *Leptodon trichomitrium* are succeeded on logs, as they become decorticated, by species of the *Hypnum* complex, *Thuidium delicatulum*, *Tetraphis pellucida*, *Hylocomium brevirostre* and *Mnium affine* var. *ciliare*. On *Tsuga* the corticolous species may remain after the logs are decorticated.

In the Tennessee Valley common corticolous bryophytes on hardwoods are: *Platygyrium repens*, *Sematophyllum adnatum*, *Orthotrichum ohioense*, *Clasmatodon parvulus*, *Leucodon julaceus* and *Drummondia prorepens*. As the trees fall and become decorticated these species are replaced by *Cephalozia curvifolia*, *Hypnum imponens*, *H. curvifolium*, and *Entodon seductrix*. Pine bark exfoliates too readily to support many bryophytes, but the logs exhibit a flora similar to that of the hardwood logs.

Successions on the butts of certain living trees in the Great Smoky Mountains have been noted by Billings and Drew (1938).

Successions on rocks are difficult to trace. Ecesis may be very slow as has been pointed out by Cooper (1937). In many cases it becomes a very difficult problem to distinguish between succession and zonation.

D. CORRELATION WITH OTHER VEGETATION

Much has been done abroad toward correlating bryophytes and bryophytic communities with other vegetation. Among the many papers which may be enumerated in this connection are those of Wisniewski (1929), Hillier (1931, 1933, 1934), Jaeggli (1933), Lippmaa (1935), Müller (1937), Ochsner (1934), Richards (1928, 1937), and Watson (1932, 1936a, 1936b). In North America less has been written on this subject. Nichols (1913, 1914,

1915, 1916, 1918) has most consistently made such correlations; more recent publications dealing with these problems are those of Taylor (1920a, 1920b), Wilson (1936), Oosting and Anderson (1937), Cain and Penfound (1938), and Cain and Sharp (1938). Particularly pertinent is the last paper which deals with certain forest types in the Great Smoky Mountains of eastern Tennessee; the report by Oosting and Anderson (1937) pertains to a neighboring area.

Because of the responses of bryophytes to micro-habitats, it is inevitable that forest types will exhibit more than one kind of bryophytic community. However, the similarity between stands of a particular bryophytic community in various stands of a forest community is quite striking. The extent of similarity which may exist is well illustrated by the *Hylocomium* communities of the spruce and fir forests of the Great Smoky Mountains. These communities have been described by Cain and Sharp (1938). In other forest types the similarities may not be so great, but we do find that certain species and communities are associated with a particular vegetation type.

It appears that some epiphytic bryophytes may be restricted to a particular type of substratum; such species may be found only in areas where certain phanerogamic substrata grow. Among the species in eastern Tennessee which seem thus restricted are: *Mylia cuneifolia*, *Bazzania nudicaulis*, *Plagiochila tridenticulata*, *Zygodon viridissimus* and *Leptodontium excelsum* which are found with extremely few exceptions on the bark of spruce and fir. *Microlejeunea Ruthii* is usually found in coniferous bark and is consequently more or less restricted to communities coniferous at least in part. Those bryophytes, such as *Neckera pennata*, *Leptodon trichomitrium* and species of *Leucodon*, which are seldom found except upon the bark of deciduous trees will be found usually in the forest types which contain such trees.

Hylocomium splendens with its associates, *Hylocomium umbratum* and *Rhytidiadelphus triquetrus*, seldom occur except on the floor of the spruce-fir forests. Wherever the trees have been cut or blown down in such forests, these mosses have disappeared. There is no evidence that they will return until the same type of forest is restored.

Other bryophytes may not be affected so directly by the vascular flora, yet may be present in particular habitats as regularly as certain phanerogams. *Pleurochaete squarrosa* is as characteristic of cedar barrens in eastern Tennessee as is *Juniperus virginiana* or *Leavenworthia uniflora*. *Dicranum condensatum* is most frequently found on siliceous rocks or sandy soils in the pine or pine-oak or dry ridges. *Weisia controversa*, *Astomum Sullivantii* and *Physcomitrium turbinatum* are typically present in the ruderal and pasture associations of the Ridge and Valley Provinces. *Calliergonella Schreberi* is found only in the spruce-fir on mountain summits or in pine forests on the Cumberland Plateau and in the Tennessee Valley. While not generally characteristic of pine stands, *Dicranum rugosum* in eastern Tennessee seems restricted to such vegetation. Associated with flood plain vegetation along rivers and creeks may be found: *Riccia fluitans*, *Notothylas orbicularis*, *Aphan-*

ortegma serratum and species of *Nanomitrium* and *Ephemerum*. Most swamp-vegetation in the mountains and on the Cumberland Plateau contains species of *Sphagnum*, and *Aulacomnium palustre*. In the marshes of the Ridge and Valley Province *Pohlia albicans*, *Hypnum Patientiae* and species of *Amblystegium* (*sensu lato*) are frequently present. Among the characteristic bog-plants of the Shady Bog in Johnson County are found *Tetraplodon pennsylvanicus* and *Calliergon cordifolium*. Further investigation will undoubtedly disclose additional correlations.

E. GEOGRAPHICAL AFFINITIES

Bryogeography began with the observation of the early bryologists. During the last half of the nineteenth century these observations became more specific, and are illustrated by the discussions of Schimper (1876) and Boulay (1877), and more recently by Herzog (1926), Amann (1928) and Bizot (1937).

In contrast to the considerable volume of work in Europe, much less has been done on the bryogeography of this continent. Herzog (1926) in his "Geographie der Moose" reviewed in a very general way the geographical distribution and relationships of bryophytes in North America. Conard (1932) recorded the occurrence of certain boreal bryophytes in Iowa. Important and most interesting are the three recent papers by Steere (1937a, 1937b, 1937c); the first and last of these deal with the occurrence of "Cordilleran" species of bryophytes on the Keweenaw Peninsula; the second discusses the distribution of *Bryoxiphium norvegicum*. Anderson (1938) gives general lists of bryophytes arranged according to physiographic regions of North Carolina. Manuals of the bryophytes of North America have given the general geographical ranges of most of our species. The "Moss Flora of North America" by Grout (1928 et seq.) is the most comprehensive and recent of these works.

A survey of the bryophytes of the Southern Appalachian Mountains and Plateaus, most species of which are recorded in the present study, indicates that the distribution in eastern North America of a majority of the species is general. However, the range of many of our species is more restricted. These species with circumscribed distribution may be classified into five groups depending on whether their affinities lie with the floras of: (1) the Northern Coniferous Forest, or (2) the Eastern Hemlock Region of Nichols (1935), or (3) the Coastal Plain including the Mississippi Embayment, or (4) the extreme southwestern portion of the United States and the tropics, or (5) the endemics of the southeastern mountain region (the Appalachian Mountains and Plateaus south of the glacial boundary). Some of these groups can be further divided.

The bryophytes with restricted ranges which occur with greatest frequency in the Northern Coniferous Forest Formation include *Hylocomium splendens*, *H. umbratum*, *Pohlia elongata*, *Sphagnum squarrosum*, *S. Girgensohnii*, *Dichodontium pellucidum*, *Oreoweisia serrulata* and *Nardia scalaris*. The

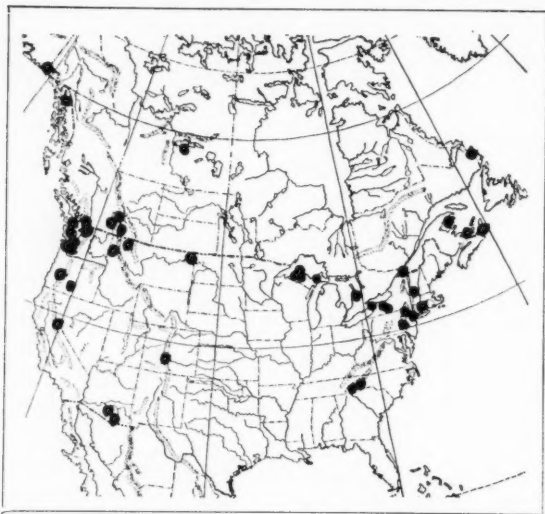


Fig. 2. Distribution of *Dichodontium pellucidum* in North America. This and the following figures are based on herbarium records unless otherwise stated.

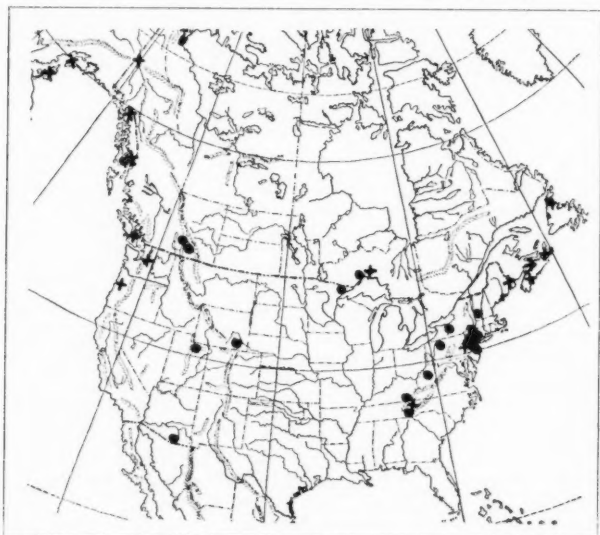


Fig. 3. Distribution of ● *Oreomeisia serrulata* and + *Nardia scalaris* in North America.

distribution of the last three have been mapped (Figs. 2 and 3) from herbarium material. Bryophytes which belong to this group but have not been reported from Central Canada are *Hygrohypnum alpestre* and *H. cochlearifolium* (Fig. 4). Lack of records of these species in Central Canada may be due to insufficient collections; on the other hand, they may have been unable to re-establish themselves rapidly in glaciated territory. These species in preglacial and interglacial epochs probably had a much wider distribution than at present. Perhaps best included with this group are certain other bryophytes characterized by a very disjunct type of distribution. Among these species whose range seems to correlate well with unglaciated regions are *Brothera Leana* (Fig. 5) and *Bryoxiphium norvegicum*. The known stations for the latter have been mapped by Steere (1937b). Examination of the lists in the following section (p. 346) of this paper will reveal additional bryophytes which are related to the Northern Coniferous Forest Formation.

The distribution of all these species has been greatly modified by glaciation. Some of the effects of the glacial epoch upon plant distribution have been pointed out for the phanerogams by Fernald (1925, 1935) and for the bryophytes by Steere (1937a, 1937b). Prior to the Pleistocene many of the listed species undoubtedly were circumboreal. Furthermore, a large number of these species were probably already present in the southern portion of the Western Cordillera and of the Appalachians (in the inclusive sense), and others may



Fig. 4. Distribution of ● *Hygrohypnum alpestre* and + *H. cochlearifolium*. The latter is reported in manuals from Washington and Wyoming.

have migrated southward along these mountains in response to cooler climate of glacial times. Thus the more southern regions and unglaciated areas in Wisconsin, Minnesota, Iowa, and other states became havens for these more northern species during this rigorous period. Subsequent to the retreat of the ice, the northward (and probably southward, from Alaska and Greenland) migration of these plants began. Some exhibited great vigor and became virtually circumpolar while others migrated more slowly and probably are still extending their ranges. Still others seemingly lacked any ability to migrate into glaciated territories, and thus today are restricted to one or several of the unglaciated areas of North America and Europe. The vigor with which species can migrate onto glaciated terrain is perhaps indicated by the progress these plants have made into the glaciated territory.

The bryophytes with restricted distribution which occur with greatest frequency in the Eastern Hemlock Region include such species as *Anomodon Rugelii*, *Plagiothecium Muellermanum* and *Cirriphyllum piliferum*. Associated species are given in the lists of the following section (p. 347). Some of these plants, such as *Herberta tenuis* and *Anoetangium Peckii*, do not occur throughout the whole Region but only from New England southward; they are, however, mainly restricted to a portion of this Region. The epiphytic species may be limited to this area in part by substratal factors. Others may be limited by the climatic conditions which control the boundaries of the Formation.

It is impossible to select bryophytes which occur with greatest frequency within the boundary of the Deciduous Forest Formations. Common species such as *Mnium cuspidatum*, *Anomodon attenuatus* and *Orthotrichum ohioense* are widely distributed in other formations.

The bryophytes with limited distribution which occur with greatest frequency in the Coastal Plain may be divided into two groups, one including

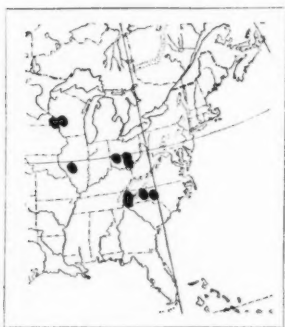


Fig. 5. Distribution of *Brothelia Leana* in North America; otherwise it is known in the Orient.

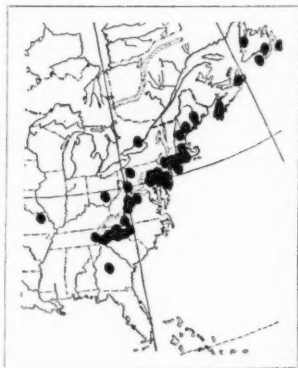


Fig. 6. Distribution of *Mnium hornum* in North America.

those of the northern Coastal Plain and the other the southern Coastal Plain. The first group includes *Mnium hornum* (Fig. 6) and *Atrichum crispum* (Fig. 7). There is some evidence that *Sphagnum Pylaeii* (Fig. 8) and *Campylostelium saxicola* (Fig. 9) are geographically related to these. The southern group embraces *Cryphaea nervosa* and *Homalotheciella fabrofolia* (Fig. 10). That certain bryophytes can be found in both the southern and northern Coastal Plains is illustrated by the distribution of *Tetraplodon pennsylvanicus* (Fig. 11). Other bryophytes of the Coastal Plain element are listed on page 347.

The presence of typically Coastal Plain plants in the Southern Appalachians was early emphasized by Kearney (1897). More recently, attention has been called to this type of distribution by Cain (1930), Camp (1938), Fer-

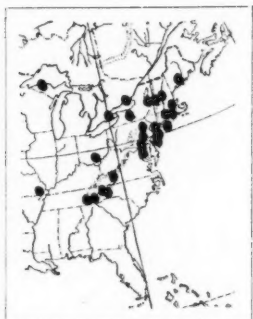


Fig. 7. Distribution of *Atrichum crispum* in eastern North America.

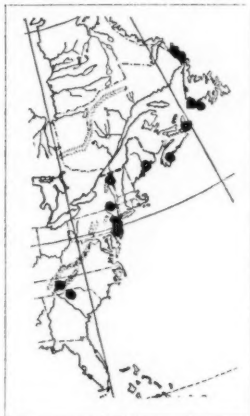


Fig. 8. Distribution of *Sphagnum Pylaeii* in North America.



Fig. 9. Distribution of *Campylostelium saxicola* in North America.

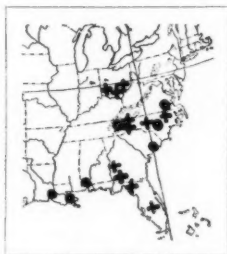


Fig. 10. Distribution of ● *Cryphaea nervosa* and + *Homalotheciella fabrofolia* in North America.

nald (1937), and Braun (1937a, 1937b). The last two authors correlate the distribution of these plants with geological history of the areas involved. While it is not denied that Coastal Plain plants may migrate into the mountains, there is much evidence that the majority of these species, including the bryophytes, were in the mountains long before the present Coastal Plain was elevated above the sea. The Southern Appalachians and certain neighboring territories have not been exposed to the action of marine waters since the Cretaceous (Fig. 36).

The occurrence of tropical bryophytes in the Southern Appalachians has been discussed in a general way by the writer (1937). These species have been divided on the basis of their presence or absence in the Coastal Plain in southeastern United States.

Fig. 11. Distribution of *Tetraplodon pennsylvanicus* in North America.

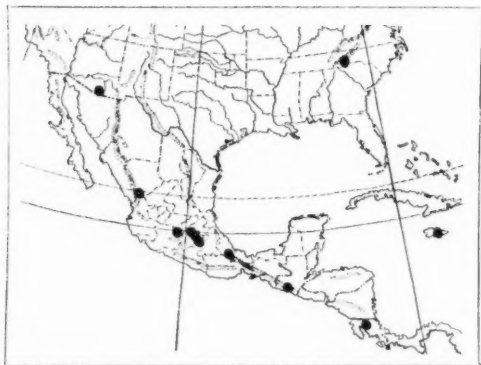
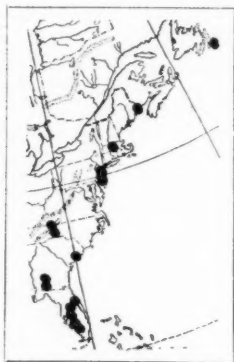


Fig. 12. Distribution of *Anoetlangium euchlorum* in the Americas north of Colombia.

Each of the tropical species which is not known from the Coastal Plain is found in the Southern Appalachians (in the inclusive sense) and in one or both of the following areas: (1) Central America, Mexico, and southwestern United States, (2) West Indies. Species which belong in this group include: *Anoetangium euchlorum*, *Campylopus introflexus*, *Drepanolejeunea bidens*, *Homalothecium Bonplandii*, *Hymenostomum tortile*, *Hookeria acutifolia*, *Leptodontium excelsum*, *L. Orcuttii*, *Merceya ligulata*, *Orthodontium pellucens*, *Tortula caroliniana*, *T. fragilis* and *Zygodon Reinwardtii*. The distribution of these species is illustrated in Figs. 12-20. In addition, *Acrobolbus rhizophyllus* and *Bartramidula carolinae* probably belong to this category. These two bryophytes, endemic to the Southern Appalachians, are

Fig. 13. Distribution of *Campylopus introflexus* in the Americas north of Colombia.

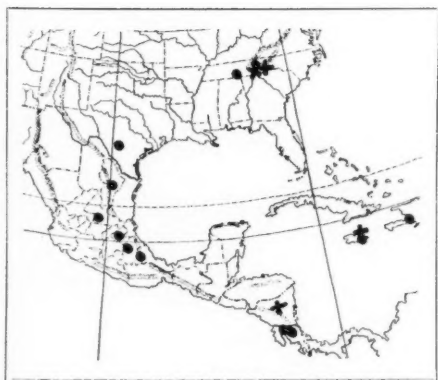
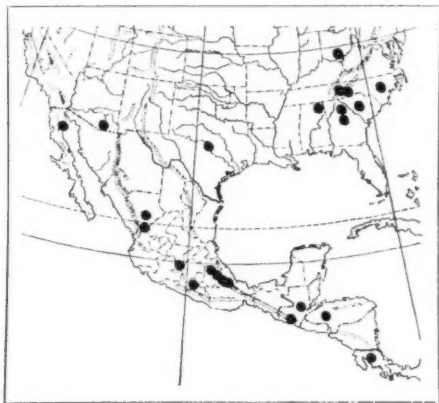


Fig. 14. Distribution of *Homalothecium Bonplandii* and *Drepanolejeunea bidens* in the Americas north of Colombia.

Fig. 15. Distribution of *Hookeria acutifolia* in the Americas north of Colombia.

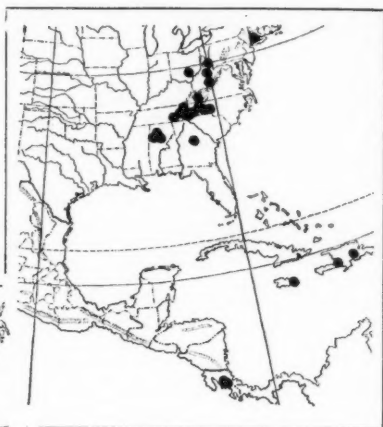
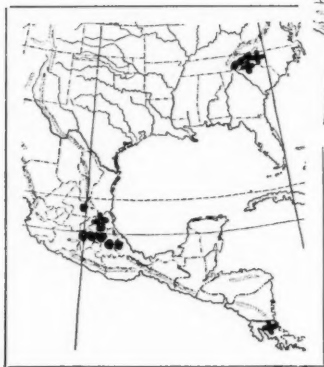


Fig. 16. Distribution of ● *Leptodontium excelsum* and + *L. Orcuttii* in the Americas north of Colombia.

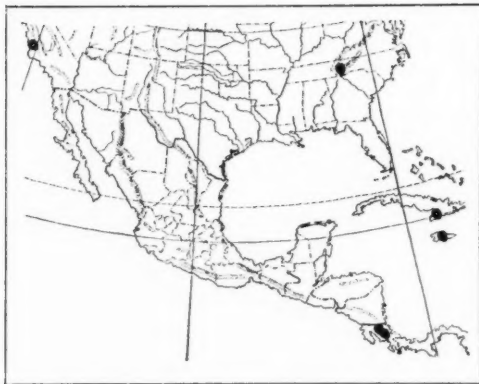


Fig. 17 Distribution of *Orthodontium pellucens* in the Americas north of Colombia.

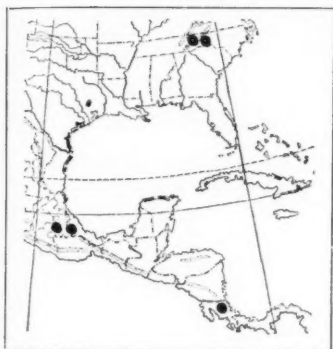


Fig. 18. Distribution of *Tortula caroliniana* in the Americas north of Colombia.



Fig. 19. Distribution of *Tortula fragilis* in the Americas north of Colombia.

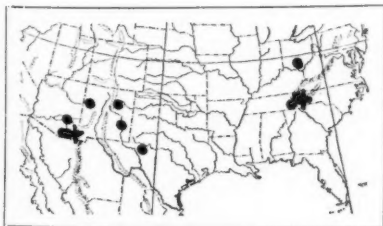


Fig. 20. Distribution of ● *Hymenostomum tortile* and + *Merceya ligulata* in North America.

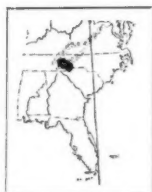


Fig. 21. Distribution of *Acrobolbus rhizophyllus* in North America. The rest of the genus in the Americas is found in South America.

there (Figs. 21 and 22) disjunct from the ranges of the other species of their respective and essentially tropical genera.

The other tropical group is represented by species which are found in the Coastal Plain of southeastern United States in addition to the areas mentioned above. Representative of such bryophytes are: *Campylopus flexuosus*, *C. tallulensis*, *Cololejeunea minutissima*, *Entodon Drummondii* (including *E. macropodus* which is closely related and on further investigation may prove to be conspecific), *Fissidens polypodioides*, *Herpetineurum toccoeae*, *Hyophila Tortula* (*H. riparia*), *Leucobryum albidum*, *Marchantia domingensis*, *Rectolejeunea Maxonii*, *Schlotheimia Sullivantii* (including *S. Mohrii*, *S. Oerstediana*, and *S. Sartorii*, all of which are closely related and perhaps conspecific (Bartram, 1934)), *Sematophyllum adnatum*, *Thuidium minutulum* (*T. Wrightii*), and *T. virginianum*. *Macromitrium Sullivantii*, *Schlotheimia lancifolia* and *Syrhopodon texanus*, all occur in North America at the north-

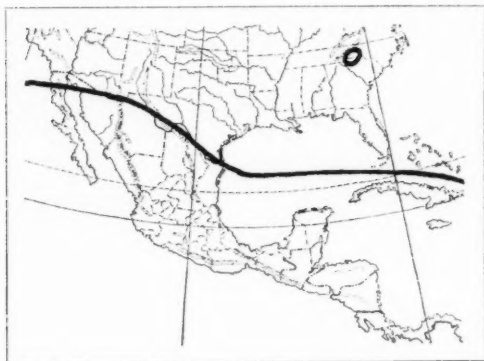
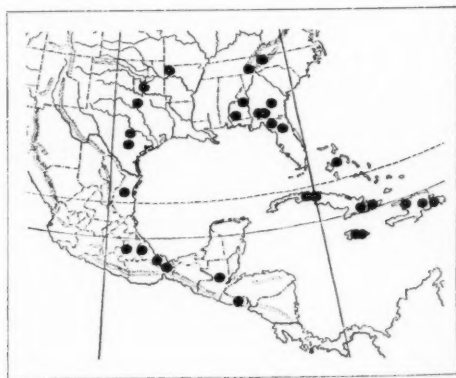


Fig. 22. The genus, *Bartramidula*, is found in the Americas north of Colombia, only south of the indicated boundary except for the single locality in North Carolina.

Fig. 23. Distribution of *Marchantia domingensis* in the Americas north of Colombia.



ern edge of the ranges of their respective genera and should possibly be included in the preceding group. *Plagiochila undata*, which occurs in the Southern Appalachians and Coastal Plain, is either closely related to or conspecific with *P. crispata* Gottsche of Mexico as pointed out by Evans (1896). The distributions of many of the above species are illustrated in Figs. 23-32.

There are three other species whose geographical affinities are less certain, which might be considered at this point. *Eucladium verticillatum* (Fig. 33) is found only on wet limestone or in calcareous springs. *Pleurochaete squarrosa* (Fig. 34) is limited to drier limestone sites and seems to be restricted in the eastern United States to the cedar barrens. The first of these two mosses may have its distribution controlled by the occurrence of wet lime-

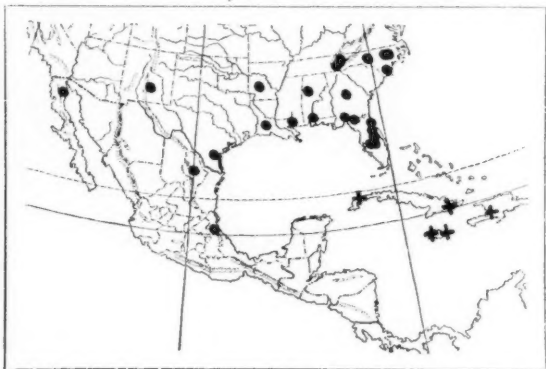


Fig. 24. Distribution of ● *Entodon Drummondii* and + *E. macropodus* in the Americas north of Colombia. These species are closely related and perhaps conspecific.

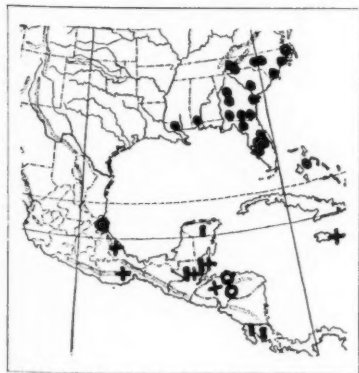


Fig. 25. Distribution of ● *Schlotheimia Sullivanii*, + *S. Mohrii*, + *S. Oerstediana* and ○ *S. Sartorii* in the Americas north of Colombia.

stone; the second, by the same factors which account for the distribution of the cedar barrens. There is some doubt whether *Tortula pagorum* (Fig. 35) is native in eastern United States; the fact that it is there found only near habitation makes it appear adventive. Eastern material should be compared carefully with western material for possible significant structural differences. An investigation of the physiological requirements of this species might prove fruitful. It is possible that smoke or soot may be a limiting factor in determining its eastern distribution.

Kearney (1900) noted the presence of tropical general and species in Tennessee. Later Fernald (1931) discussed the geographical relationships of certain Southern Appalachian and tropical phanerogams and noted the correlation between their distribution and the geological age of the areas in which they were found. A comparison of the distribution maps of the dis-

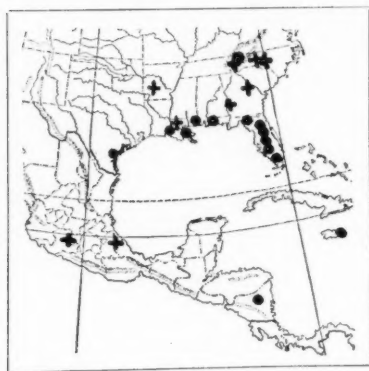
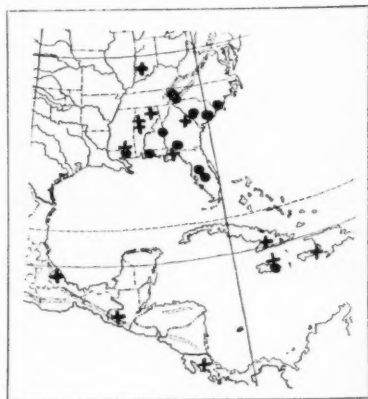


Fig. 26. Distribution of *Rectolejeunea minutissima* and *Herpetineurum loccoae* in the Americas north of Colombia.

Fig. 27. Distribution of *Rectolejeunea Maxonii* and *Fissidens polypodioides* in the Americas north of Colombia.



junct tropical bryophytes (Figs. 12-20) with Fig. 36 shows that these species are found in or close to areas which have not been exposed to the action of marine waters since the Cretaceous. Moreover, it is not difficult to hypothesize the migration of many species (Figs. 23-32) to the Coastal Plain in

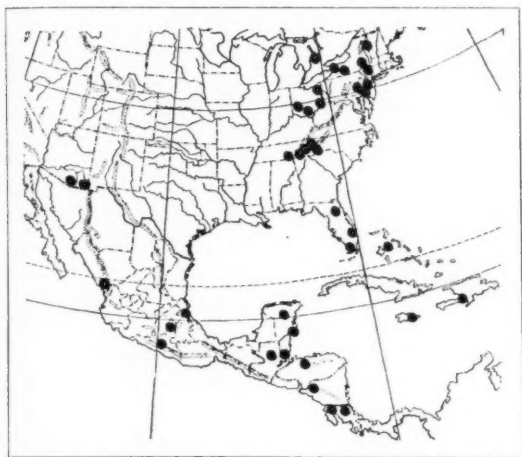


Fig. 28. Distribution of *Hyophila Tortula* in the Americas north of Colombia.



Fig. 29. The line marks the approximate northern limit of occurrence of *Leucobryum albidum*. Data from publications as well as herbaria were considered.



Fig. 30. The line marks the approximate northern limit of occurrence of *Sematophyllum adnatum*. Data from publications as well as herbaria were considered.

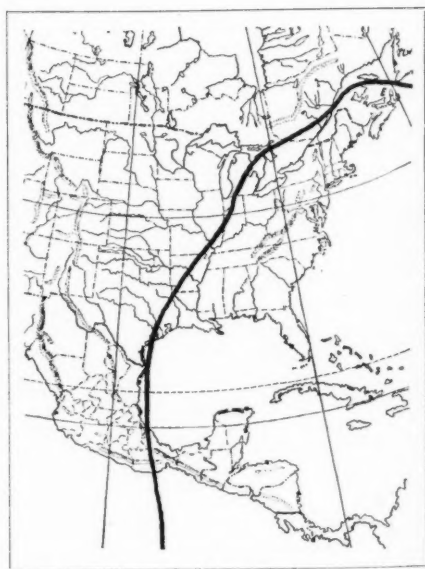


Fig. 31. The line marks the approximate northern and western limit of occurrence of *Thuidium minutulum*. Data from publications as well as herbaria were considered.

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Fig. 30. The line marks the approximate northern limit of occurrence of *Sematophyllum adnatum*. Data from publications as well as herbaria were considered.

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post-Cretaceous times. Thus it would seem that many if not most of these so-called tropical bryophytes are representative of a once probably widespread Tertiary Flora.

One of the puzzling features of the distribution of these tropical bryophytes is their apparent absence from the Ozark Highland, Ouachita Mountains, and the mountains of western United States (see Fig. 36). More intensive collecting in these areas would aid in the solution of this problem.

It is interesting, and probably significant, that in contrast to the temperate and boreal bryophytes, only seven (*Fissidens polypodioides*, *Hookeria acutifolia*, *Hyophila Tortula*, *Leucobryum albidum*, *Sematophyllum adnatum*, *Thuidium minutulum* and *T. virginianum*) of the thirty-one species cited



Fig. 32. Distribution of ● *Syrrhopodon texanus*, ○ *Schlotheimia lancifolia* and + *Macromitrium Sullivantii* in North America. Each is a species lying at the northern boundaries of the areas occupied by their respective and essentially tropical genera.

Fig. 33. Distribution of *Eucladium verticillatum* in North America and the West Indies.



above as exhibiting definite tropical affinities have extended their ranges, in eastern North America, northward into the glaciated territory. The northernmost stations for four of these, *Fissidens polypodioides* (Fig. 27), *Hookeria acutifolia* (Fig. 15), *Leucobryum albidum* (Fig. 29), and *Sematophyllum adnatum* (Fig. 30) are not far from the glacial boundary (Fig. 36). Moreover, it is probable that the Indiana station for the *Fissidens* does not lie north of the Wisconsin boundary, for Steere (1937b) quotes from a letter of Malott, saying that the Ferncliff locality "is just beyond the limits of the Wisconsin boundary."

Much has been written about the relationship between certain of the phanerogams of southeastern United States and eastern Asia. Among the few bryophytes which have been noted as having distributions paralleling those of vascular plants are: *Herpetineurum toccoeae*, *Brothera Leana*, *Drummondia prorepens*, *Anomodon tristis* and *Homalia Sharpii* whose apparently nearest relative is *H. Targioniana*. Others are listed by Sullivant and Lesquereux (1859).

Adams (1902) suggests that the southeastern states were a center of geographical distribution of flora and fauna. It is certainly true that the Southern Appalachians served as an area from which many species of both phanerogams and bryophytes migrated to the Coastal Plain in post-Cretaceous times and to the north in post-glacial times. Reference to the last part of the following section will indicate other species which are still restricted (endemic) to the Southern Appalachians.

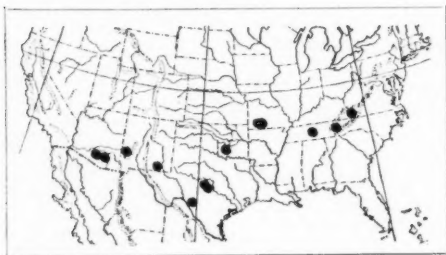


Fig. 34. Distribution of *Pleurochaete squarrosa* in North America.

Fig. 35. Distribution of *Tortula pagorum* in North America.

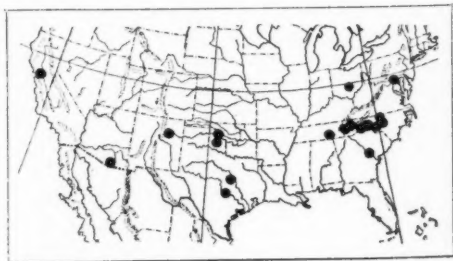




Fig. 36. Areas stippled and in solid color are those regions which have not been exposed to the action of marine waters or glacial ice since the Cretaceous. The boundaries are approximate. This map was made by superimposing several from Schuchert (1935) and one from Fernald (1931). The dotted line marks the northern boundaries of the ranges of most tropical bryophytes in western North America.

F. CLASSIFIED LISTS OF GEOGRAPHICALLY SIGNIFICANT
SOUTHERN APPALACHIAN BRYOPHYTES

The following classified lists of geographically-significant bryophytes which occur in the Southern Appalachians has been prepared with the full knowledge that it is incomplete and to some extent probably inaccurate. As a result of further botanical exploration certain species may have to be stricken from the lists or moved from one category to another.

Correlated lists of fungi and vascular plants are being prepared but at the present time are incomplete.¹ Those interested in correlating the distribution of vascular plants with that of the Southern Appalachian bryophytes should see the papers of Cain (1930), Jennison (1935), Braun (1937a, 1937b), Fernald (1937) and Camp (1938), and monographs such as those of Pennell (1935), Barkley (1937), and Svenson (1929, 1932, 1934, 1937).

The division into geographical groups essentially follows that outlined in the previous section (p. 329). It should be emphasized that the species are not generally distributed, but at the same time they are not always completely restricted to the area indicated nor are they always widely distributed within the designated region.

I. Bryophytes with greatest frequency of occurrence in the Northern
Coniferous Forest Formation.

Blindia acuta (Hedw.) B.S.G.
Brachythecium rutabulum (Hedw.) B.S.G.
Campyllum polygamum (B.S.G.) Bryhn
Dichodontium pellucidum Schimp.
Dicranum rugosum Brid.
Depranocladus exannulatus (Guemb.)
Warnst.
Drepanocladus Sendtneri (Schimp.)
Warnst.
Hygrohypnum dilatatum (Wils.) Loeske
Hygrohypnum eugyrium (B.S.G.) Loeske
Hygrohypnum luridum (Hedw.) Dix.
Hygrohypnum ochraceum (Turn.) Loeske
Hylacomium splendens (Hedw.) B.S.G.
Hylacomium umbratum (Hedw.) B.S.G.
Hypnum Crista-castrensis Hedw.
Hypnum fertile Sendt.

Hypnum reptile Mx.
Myurella Careyana Sull.
Myurella julacea (Schwaegr.) B.S.G.
Nardia scalaris S. F. Gray
Oreoweisia serrulata (Funck.) De Not.
Paraleucobryum longifolium (Hedw.)
Loeske
Plagiothecium elegans (Hook.) Sull.
Plagiothecium striatellum (Brid.) Kindb.
Pohlia elongata (Hedw.) Brid.
Rhabdoweisia denticulata (Brid.) B.S.G.
Rhytidiadelphus squarrosus (Hedw.)
Warnst.
Seligeria Doniana (Sm.) C. Muell.
Sphagnum Girgensohnii Russ.
Sphagnum squarrosus Crome

II. Disjuncts but probably formerly allied with those of the Northern
Coniferous Forest Formation.

Amblystegiella confervoides (Brid.)
Loeske
Anomodon tristis (Cesati) Sull.
Bazzania denudata (Torr.) Trevis
Bazzania tricenata (Wahlenb.) Trevis
Brothera Leana (Sull.) C. Muell.
Bryoxiphium norvegicum (Brid.) Mitt.

Dicranodontium asperulum (Mitt.) Broth.
Grimmia teretineris Limpr.
Hygrohypnum alpestre (Hedw.) Loeske
Hygrohypnum cochlearifolium (Vent.)
Broth.
Plagiothecium lactum B.S.G.
Zygodon viridissimus (Dick.) Brown

¹ Preliminary lists may be found in the original dissertation, Sharp (1938b).

III. Species whose greatest frequency of occurrence is in the Eastern Hemlock Region of Nichols.

Anoetangium Peckii Sull.
Anomodon Rugelii (C. Muell.) Kiessl.
Bryhnia novae-angliae (S. & L.) Grout
Cirriphyllum piliferum (B.S.G.) Grout
Dichelyma capillaceum Myr.
Grimmia Olneyi Sull.
Herberta tenuis Evans
Heterophyllum Haldanianum (Grev.) Kindb.
Homalia Jamesii Schimp.
Hygrohypnum novae-caesariae (Aust.) Grout
Lophozia excisa (Dicks.) Dum.
Microlejeunea ulicina (Tayl.) Evans

Mylia cuneifolia Spruce
Neckera complanata (Hedw.) Hueben.
Plagiochila tridenticulata Tayl.
Plagiothecium Muellerianum Schimp.
Pleuroidium palustre (B.S.G.) B. S. G.
Pseudisothecium myosuroides (Brid.) Grout
Radula tenax Lindb.
Sematophyllum marylandicum (C. Muell.) E. G. Britt.
Thuidium pygmaeum B.S.G.
Tortula Porteri (James & Aust.) Broth.
Uloa Ludwigii Brid.

IV. Species whose greatest frequency of occurrence is in the Coastal Plain (including the Mississippi Embayment).

Atrichum crispum James
Campylostelium saxicola (W.&M.) B.S.G.
Crossolejeunea bermudiana Evans
Cryphaea glomerata Schimp.
Cryphaea nervosa (Hook. & Wils.) B.S.G.
Fabronia Ravenelii Sull.
Funtinalis Sullivanii Lindb.
Homalotheciella fabrofolia (Grout) Broth.

Mnium hornum Hedw.
Plagiothecium micans (Sw.) Paris
Radula calousiensis Aust.
Sphaerocarpus texanus Aust.
Sphagnum Pylaeii Brid.
Tetraplodon pennsylvanicus (Brid.) Sayre
Tortula plinthobia (S. & L.) Broth.

V. Bryophytes with their greatest frequency of occurrence in tropical or subtropical North America.

**Acrobolbus* as a genus
 **Anoetangium euchlorum* (Schwaegr.) Mitt.
Barbula Cruegeri Sond.
 **Bartramidula* as a genus
Campylopus flexuosus Brid.
 **Campylopus introflexus* Brid.
Campylopus tallulensis S. & L.
 **Drepanolejeunea bidens* (Steph.) Evans
Entodon Drummondii (B.S.G.) Jaeg. when considered with *E. macropodus* (Hedw.) C. Muell.
Fissidens polypodioides Hedw.
Herpetineurum toccocae (S. & L.) Card.
 **Heterophyllum nemorosum* (Koch) Kindb.

**Homalothecium Bonplandii* (Hook.) J. & S.
 **Hookeria acutifolia* Hook.
 **Hymenostomum tortile* (Schwaegr.) B.S.G.
Hyophila Tortula (Schwaegr.) Hampe
 **Leptodontium excelsum* (Sull.) E. G. Britt.
 **Leptodontium Orcuttii* Bartr.
Leucobryum albidum (Brid.) Lindb.
Leucolejeunea uniloba (Lindb.) Evans
Macromitrium as a genus
Marchantia domingensis (Lehm. & Lindenb.)
 **Merceya ligulata* (Spruce) Schimp.
 **Metzgeria hamata* Lindb.
Metzgeria myriopoda Lindb.

* Species so marked are not yet known from the Coastal Plain of southeastern United States.

**Orthodontium pellucens* (Hook.) B.S.G.
Pallavicinia Lyellii (Hook.) Gray
Philonotis longiseta (Rich.) E. G. Britt.
Plagiochila undata Sull. when considered
 with *P. crispata* Gottsche.
Plagiothecium micans (Sw.) Paris
Radula andicola Steph.
Rectolejeunea Maxonii Evans
Schlotheimia as a genus

Sematophyllum adnatum (Mx.) E. G. Britt.
Syrrophodon as a genus
Thuidium minutulum B. S. G.
Thuidium virginianum (Brid.) Lindb.
 **Tortula caroliniana* Andrews
 **Tortula fragilis* Tayl.
Trematodon longicollis Mx.
 **Zygodon Reinwardtii* (Hornsch.) A. Br.

VI. Species endemic to the Southern Appalachians and closely neighboring areas.

Acrobolbus rhizophyllus Sharp
Bartramidula carolinae Sharp
Bazzania nudicaulis Evans
Diplophyllum Andrewsii Evans
Entodon Sullivantii (C. Muell.) Lindb.
Euosmolejeunea Evansii M. S. Taylor
Fabronia imperfecta Sharp
Homalia Sharpii Williams

Macromitrium Sullivantii C. Muell.
Oncophorus Raui (Aust.) Grout
Porella wataugensis Sull.
Radula Sullivantii Aust.
Riccardia incurvata (Lindb.) Steph.¹
Schlotheimia lancifolia Bartr.
Tortula propagulosa Sharp

G. SUMMARY

The large number of bryophytes in eastern Tennessee may be accounted for by the great diversity of microclimates and variety of substrata which facilitated the survival of many species of the floras which have penetrated the area since Cretaceous times. A majority of the bryophytes are generally distributed in eastern North America. Many species, however, are more circumscribed in their range and these may be divided into five major categories based upon their geographical relationships. Approximately ten per cent of eastern Tennessee bryophytes exhibit affinities with the vascular flora of the Northern Coniferous Forest; more than five per cent, with that of the Eastern Hemlock Region; more than three per cent, with the Coastal Plain flora; approximately ten per cent, with that of the subtropics and tropics; and more than three per cent are endemic to the Southern Appalachians. Further subdivision is possible in some cases. The circumscribed distribution of the geographically important species may be due either to climatic or to prehistoric factors.

Bryophytes may serve as pioneer plants and the bryophytic invaders of eastern Tennessee are listed for various substrata under diverse moisture conditions. Succession of bryophytic communities is recorded for a number of habitats but it is admitted that it is frequently difficult to distinguish between succession and zonation.

Many eastern Tennessee bryophytes are limited to certain vegetation types. This restriction may be correlated frequently with substratal or climatic factors. Because of this limitation, bryophytes serve at times as useful indicators of moisture-content, pH or other conditions of the habitat.

¹ Found also in Europe.

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Bryophyta of Arctic America. II.

Species collected by J. Dewey Soper, principally in
southern Baffin Island.¹

William Campbell Steere

The bryophyte flora of the Canadian Arctic Archipelago remains very incompletely known, even after more than a century of botanical exploration there. The primary reason seems to be that in large part plant collections have been made only incidentally to geographical exploration or some other non-botanical activity.

Although Baffin Island is one of the largest islands in the world, accessible enough so that its colonization has been considered (Millward, 1930), its bryophyte flora is less well known than of other Arctic islands much farther north, because most of the recent scientific exploring expeditions have gone to Ellesmere and Devon Islands.

However, a search through the literature reveals a number of scattered, unrelated reports of bryophytes from Baffin Island. Of the many English expeditions sent out in search for a Northwest Passage to the Orient, north of the American Continent, the Ross Expedition of 1818 provided the first known plants (including bryophytes) from the American Arctic regions (Brown, 1819). Five mosses, *Polytrichum juniperinum*, *Orthotrichum cupulatum*? (probably *O. microblepharum*), *Trichostomum (Rhacomitrium) lanuginosum*, *Dicranum scoparium*, *Mnium (Aulacomnium) turgidum*, were collected "on the coasts of Baffin's Bay, from Lat. 70° 30' to 76° 12', on the East Side; and at Possession Bay in Lat. 73°, on the West Side." Which of the species were collected at Possession Bay, on Bylot Island, at the north-eastern end of Baffin Island, is not known, because of the imperfect documentation of the specimens and the ambiguous manner in which they are reported. Fortunately, all the species reported are widely distributed in the American Arctic, so that no special problems of critical distribution are left unsettled.

The second Parry Expedition (1821-1823) made a large collection of bryophytes in the eastern Arctic (Hooker, 1825), including two stations on Baffin Island. From the west side ("Northeast coast of America, Lat. 67½° North") are reported "*Bryum caespitium*, foliis acuminatis, capsulis elongatis," whose present status is probably indeterminable, *Didymodon (Distichum) capillaceum*, *Haplodon Wormskioldii* "folia acutiuscula," *Splachnum (Tetraplodon) urceolatum*, and *Voitia hyperborea*. From Upper Savage Island, on the south coast of Baffin Island, is reported "*Dicranum virens*,"

¹ Papers from the Department of Botany and the Herbarium of the University of Michigan, No. 679.

which probably represents *Oncophorus Wahlenbergii*, a very common species in the American Arctic, and at one time included as a form or variety of *O. virens*, which is extremely rare in the same region. Although the third Parry Expedition (1824-1825) collected plants at Port Bowen, on the Brodeur Peninsula of northwestern Baffin Island, no bryophytes from this locality are included among the very few species listed in the report of the expedition.

The surprisingly large number of expeditions which were sent out officially and privately in search of Sir John Franklin, who was lost with his two ships and entire party, apparently collected very few plants on Baffin Island, but concentrated their efforts on the islands farther west and north. However, from the collections made by several different "Franklin Searching Expeditions," Hooker (1857) has reported the following species from Pond's Bay and Navy Board Inlet, in northern Baffin Island: *Jungermannia* (*Lophozia*) *barbata*, J. (*Blepharostoma*) *trichophylla*, *Plagiochila asplenioides*, *Frullania Tamarisci*, *Distichium capillaceum*, *Dicranum elongatum*, *Trichostomum* (*Didymodon*) *rigidulum*, *Bryum* (*Pohlia*) *nutans*, *B. pseudotriquetrum*, *Mnium hymenophylloides*, *Hypnum* (*Myurella*) *julaceum*, H. (*Orthothecium*) *chryseum*, H. (*Brachythecium*) *salebrosum*, H. (*Amblystegiella*) *Sprucei*, H. (*Campylium*) *stellatum*, and H. (*Drepanocladus*) *unicatum*.

The whaling industry in Arctic American waters, which reached its greatest development during the second half of the nineteenth century, was, of course, completely utilitarian and the work extremely dangerous, so that very little plant collecting or other scientific work was done. The one outstanding exception is the work of James Taylor (1862, 1863) who, during the years of 1856, 1857, 1858 and 1861, made very considerable collections of plants on Baffin Island, including the largest number of species of Bryophyta known at the time from the American Arctic (Dickie, 1869).

Taylor delimits the area over which he collected as follows:

On the east side of Davis Straits the space examined extends from Disco Island to the southern part of Melville Bay; and on the west side, from Cape Enderby to Pond's Bay. On the east side the excursions were chiefly along the coast, rarely exceeding two miles inland; on the west side also the coast-line alone was explored, excepting at Cape Searle and Cumberland Sound, where explorations were made as far as five or six miles inland. With more time and better arrangements for penetrating further, a much more extensive collection might have been made.

The species reported from Baffin Island are:

Gymnomitrium concinatum, *Sarcoscyphus Erhardii* (*Marsupella emarginata*), *Scapania nemorosa*, *Jungermannia* (*Tennomma*) *setiformis*, J. (*Sphenobolus*) *minuta*, J. (*Lophozia*) *barbata*, J. *islandica* (*Pleuroclada albens* var. *islandica*), J. *divaricata* (*Cephalozia* *byssacea*), *Ptilidium ciliare*, *Marchantia polymorpha*, *Andreaea petrophila*, A. *Blyttii*, *Sphagnum acutifolium*, S. *fimbriatum*, S. *rubellum* (S. *capillaceum* var. *tenellum*), *Voitia hyperborea*, *Weissia* (*Dicranoweissia*) *crispula*, *Cynodontium polycarpum*, C. *virens* β *Wahlenbergii* (*Oncophorus Wahlenbergii*), *Dicranum elongatum*, D. *fuscescens*, *Blindia acuta*, *Anacalypta* (*Stegonia*) *latifolia*, *Distichium capillaceum* and var. β *brevifolium*, D. *inclinatum*, *Ceratodon purpureus*, *Desmatodon systilius*, *Barbula* (*Tortella*) *fragilis*, B. (*Tortula*) *mucronifolia*, *Grimmia apocarpa*, G. *platyphylla*, G. *pulvinata*, G. *apiculata*, G. *elongata*, *Racomitrium lanuginosum*, *Amphoridium* (*Amphidium*) *lapponicum*, *Ulota curvifolia* (?), *Orthotrichum speciosum* (?), *O. arcticum*, *Encalypta rhabdocarpa*, E. *ciliata*, *Tayloria splachnoides* var. γ *angusti-*

folia (*T. acuminata*), *Tetraplodon mnioides*; *Splachnum* (*Haplodon*) *Wormsköldii*, *Leptobryum pyriforme*, *Webera polymorpha* (*Pohlia acuminata*), *W. (Pohlia) nutans*, *W. (Pohlia) cruda*, *W. (Pohlia) Ludwigii* and var. β *gracile* (*Pohlia gracilis*), *Bryum arcticum*, *B. purpurascens*, *B. calophyllum*, *B. bimum*, *B. pallidum*, *B. argenteum*, *Zieria (Plagiobryum) demissa*, *Mnium rostratum* (?), *M. serratum*, *M. hymenophylloides*, *Messea uliginosa*, *Aulacomnium palustre*, *A. turgidum*, *Bartramia ithyphylla*, *B. pomiformis*, *Conostomum boreale*, *Oligotrichum hercynicum*, *Psilopilum arcticum*, *Pogonatum (Polytrichum) alpinum*, *P. dentatum*, *Polytrichum piliferum*, *Myurella julacea*, *Orthothecium rubellum*, *O. rufescens*, *Camptothecium (Tomenthypnum) nitens*, *Plagiothecium pulchellum*, *Hypnum (Drepanocladus) Kneiffii*, *H. (Drepanocladus) exannulatum*, *H. (Drepanocladus) fluviatile*, *H. (Drepanocladus) revolvens*, *H. (Drepanocladus) uncinatum*, *H. reptile*, *H. hamulosum*, *H. (Calliergon) sarmentosum*, and *H. (Calliergon) turgescens*.

Taylor was apparently the first collector in the American Arctic to furnish first-hand notes concerning the habitats of his specimens and the association of species. His account, which follows, is the first description of the habitats of American Arctic mosses, yet in spite of its very brief nature, has not been much improved upon until relatively recently. He says:

The variety of surface is very considerable; lofty hills, valleys and deep ravines abound; in some districts are extensive plains covered with shingle, where *Conostomum boreale* and *Racomitrium lanuginosum* are in the greatest profusion; again, there are large tracts where *Ceratodon purpureus* and *Psilopilum arcticum* are plentiful. Elsewhere, at various elevations, there are morasses and peat-bogs, where species of *Sphagnum* and other aquatic mosses find a suitable habitat. In other quarters we meet with steep cliffs, in the crevices of which, along with ferns and other plants, there grow various species of *Bryum* and *Hypnum*; the numerous boulders of various sizes are covered with tufts of *Andreaea*, etc.

The account of Taylor's collections of bryophytes was published in a well-known scientific journal (*Journal of the Proceedings of the Linnean Society, Botany*), but in spite of its obvious importance seems to have escaped the notice of most or all later workers. This lapse is still more puzzling since Taylor himself in his publications dealing with the flowering plants (1862, 1863) makes the statement: "I collected a great many mosses and lichens." Furthermore, Mitten (1865) described as new three species from Taylor's collection, *Grimmia platyphylla*, *Stereodon rubellus*, and *S. plicatilis*, and mentioned several others. Mitten's references to specimens from "Davis's Straits, Taylor," have been widely copied and appear in most American catalogues and manuals of bryophytes (Lesquereux and James, 1884; Macoun, 1892, 1902; Grout, 1928-1938; etc.).

Most of the expeditions of the last part of the nineteenth century and the earlier part of this one were for the purpose of attaining the North Pole or at least "farthest north," and did not concern themselves with relatively accessible Baffin Island, with the notable exception of the Canadian Expeditions. Although the German Polar Expedition of 1882-1883 wintered in Cumberland Sound, I can find no record of mosses collected (Ambronn, 1890).

England in 1880 ceded to the Dominion of Canada all claims to British territory to the north of continental North America, between longitudes 60° and 140° W., northward to the Pole. The Canadian Government at once began systematic investigations and explorations of their new Arctic pos-

sions. The first reports of Arctic bryophytes resulting from the Canadian Arctic Expeditions seem to be those of Dr. Bell (1884, 1901) in which unfortunately the collection data are very often ambiguous or lacking, usually because of the arrangement of the species in tables. In the 1884 report, *Sphagnum acutifolium*, *Racomitrium lanuginosum*, *Bryum arcticum*, and *B. Brownii* are tabulated as coming from "Cape Prince of Wales and Ashe's Inlet, or North Bluff, in the middle of the straits." This curious grouping of localities is almost completely useless for phytogeographical purposes because Cape Wales is in northernmost Quebec, on the south side of Hudson Strait, and Ashe's Inlet is on the northern side, along the south shore of Baffin Island, on Big Island. In a later report, Bell (1901) listed: *Ceratodon purpureus*, *Racomitrium lanuginosum*, *Barbula (Tortella) fragilis*, *Amphoridium (Amphidium) lapponicum*, *Tetraplodon mnioides*, *Webera (Pohlia) nutans*, *Bryum arcticum* and *Aulacomnium palustre* from the south coast of "Baffin Island between Amadjuak Bay and Chorkback Inlet" (about Lat. $64^{\circ} 64' 50''$ N., Long. $73^{\circ} 74' 50''$ W.). Many of Dr. Bell's specimens have been re-reported, with more complete habitat and geographical data, by Macoun in his "Catalogue of Canadian Plants" (1892, 1902) where other collections are reported for the first time. In the two publications, the following species are listed as having been collected in southern Baffin Island (1892): *Racomitrium lanuginosum*, *Aulacomnium turgidum*, and (1902) *Ceratodon purpureus*. N. C. Kindberg (Ottawa Naturalist, 1893-1910) also reported several species of Bryophyta collected on Baffin Island by Dr. Bell and Commander A. P. Low, but his identifications are so generally unreliable and the species reported so improbable that they are better omitted here. Two mosses, *Aulacomnium palustre* and *Pohlia nutans* are mentioned incidentally as having been collected at Ashe's Inlet, Big Island, on the south coast of Baffin Island, in a report on some plants from much farther west, collected by Tyrrell (1898).

One of the latest reports of bryophytes from Baffin Island concerns the collections of Seidenfaden (Harmsen and Seidenfaden, 1932) made in 1928. Twenty-four species are listed from Totnes Road, Exeter Sound (Lat. $66^{\circ} 27' 27''$ N., Long. $62^{\circ} 18' 18''$ W.), as follows:

Anthelia julacea, *Cephalozia Starkei* (C. byssacea), *Lophozia ventricosa*, *Sphenobolus minutus*, *Chandonanthus (Temnoma) setiformis*, *Lophozia (Tritomaria) quinque-dentata*, *Martinellia (Scapania) curta*, *Cymnomitrium concinatum*, *Sphagnum acutifolium*, *Dicranella cerviculata*, *Dicranum elongatum*, *D. fuscescens*, *Racomitrium aciculare*, *R. lanuginosum*, *R. canescens*, *Webera (Pohlia) nutans*, *Aulacomnium turgidum*, *A. palustre*, *Philonotis tomentella*, *Drepanocladus intermedius*, *Philocarya aspera*, *Polytrichum alpinum*, *P. piliferum*, and *P. sexangulare*.

The authors say:

As far as we have been able to find out, Baffin Island was fully unknown with respect to mosses prior to our visit there in 1928. . . . so the following list of the mosses on Baffin Island is probably the first one ever published."

Because they were unaware of the many previous collections and publications concerning the bryophytes of Baffin Island just cited, Harmsen and Seidenfaden incorrectly annotated many of their species, which had been previously reported from Baffin Island, as "New to Arctic America."

Very recently, Hesselbo (1937), in the report of plants collected by the Fifth Thule Expedition, has published an account of the large collection of Bryophyta made in Arctic Canada by several collectors, both on the mainland and among the Arctic Islands, including many stations in northern Baffin Island (Cockburn Land). The species listed are:

Blepharostoria trichophyllum, *Lepidozia setacea* var. *sphagnicola*, *Cephaloziella Hampeana*, *Haplozia* (*Jungermannia*) *sphaerocarpa*, *Lophozia* (*Orthocaulis*) *Kunzeana*, *Sphenobolus minutus*, *Lophozia* (*Tritomaria*) *quinquedentata*, *Cephalozia bicuspidata*, *C. pleniceps*, *Sphagnum rubellum* (*S. capillaceum* var. *tenellum*), *Ceratodon purpureus*, *Ditrichum flexicaule*, *Dicranum elongatum*, *D. congestum*, *D. spadiceum*, *Didymodon rubellus*, *Tortula ruralis*, *Racomitrium hypnoides* (*R. lanuginosum*), *Pohlia nutans*, *Bryum crispulum*, *B. ventricosum*, *Mnium cuspidatum* (L.) Neck. (*M. affine*), *Cinclidium arcticum*, *Gymnocybe* (*Aulacomnium*) *palustris*, *G. (Aulacomnium) turgida*, *Messecia trichodes* (*M. uliginosa*), *Philonotis tomentella*, *Timmia austriaca*, *Orthotrichum Killiasii*, *Myurella julacea*, *Thuidium (Abietinella) abietinum*, *Amblystegium (Campyllum) polygamum*, *A. (Campyllum) stellatum*, *Calliergon turgescens*, *Hypnum (Calliergidium) pseudostamineum*, *H. (Drepanocladus) uncinatum*, *Brachythecium plumosum*, *Camptothecium trichoides* (*Tomenthypnum nitens*), *Curriphyllum cirrhosum*, *Eurhynchium strigosum*, *Orthothecium chryseum*, *Plagiothecium pulchellum*, *Stereodon (Hypnum) revolutus*, *Hylocomium proliferum* (*H. splendens*), *Polytrichum alpinum* and *P. strictum*.

During the last few years botanical exploration of the Canadian Arctic Archipelago has been going on at a much more rapid rate, and as a result several fine collections of bryophytes have been made. Dr. Nicholas Polunin (Steere, 1939) and Père Arthème Dutilly have made large collections of mosses and hepatics, not only on Baffin Island, but on others of the Arctic Islands. Dr. David Potter, botanist to the 1937 MacMillan Expedition, collected a few bryophytes in southeasternmost Baffin Island, although the greater part of his collections were made along the coast of Newfoundland Labrador. These collections will be reported upon later.

Insofar as the bryophytes of Baffin Island, especially the southern part, are concerned, among the most important collections ever made are those of J. Dewey Soper, now Chief Federal Migratory Bird Officer of the Prairie Provinces of Canada. Over a period of several years, in the course of three expeditions to Baffin Island, Mr. Soper (1928, 1930) made the collections which are the subject of the following list.

On behalf of the National Museum of Canada, as naturalist to the Canadian Arctic Expedition of 1923, he collected Bryophyta at Pangnirtung Fiord, Cumberland Sound, at Pond Inlet, and at Strathcona Sound, all in Baffin Island; at Craig Harbour, Ellesmere Island; at Beechey Island and Dundas Harbour, North Devon Island; and in western Greenland. The 1923 trip was a reconnaissance affording few opportunities for the collection of specimens, so July 5, 1924, again in behalf of the National Museum of Canada, Mr. Soper sailed from Quebec on the C. G. S. "Arctic," reaching Panenirtung Fiord, Cumberland Sound, Baffin Island, on July 22, where he made his headquarters for two years. Mr. Soper spent the remainder of 1924 about Cumberland Sound, and from mid-April to late September of 1925 in an exploration of the country about Nettiing Lake and the Koukdjuak River to the west of Cumberland

Sound. April 11, 1926, he left Pangnirtung Fiord on an overland trip to Hudson Strait, which he reached at Amadjuak Bay April 26 and Cape Dorset May 20. After spending the summer in the vicinity of Cape Dorset and more than two years on Baffin Island, Mr. Soper left the Arctic. In 1928, the Canadian Department of the Interior, acting through the Northwest Territories and Yukon Branch, and the National Parks Branch, which administers the Migratory Birds Convention Act in Canada, sent Mr. Soper back to Baffin Island, to conclude his search for the nesting grounds of the Blue Goose. He made his headquarters at Cape Dorset and spent the fall and winter in geographical exploration, traversing and mapping the coast and interior of the Foxe Peninsula and the west coast of Baffin Island to Lat. $67^{\circ} 40' N.$ May 17, 1929, he left Cape Dorset, travelled down Hudson Strait to Chorkbak Inlet, followed that to its northwestern extremity in Terreuya Bay, and thence directly across the Foxe Peninsula to a point on the west coast of Baffin Island north of Bowman Bay. Here, on the bank of a tundra stream near Foxe Basin, Camp Kungovik (after the Eskimo name for the Blue Goose) was established in Lat. $65^{\circ} 35' N.$ Mr. Soper returned to Cape Dorset August 17, after the successful completion of his mission, and left Lake Harbour for Ottawa a week later. Although his primary interest during his extensive travels in Baffin Island had been zoological, and many hardships were encountered, Mr. Soper's collections of Bryophyta are notable for their critical selection, careful preparation, and generous size. For help in finding the localities just mentioned in Mr. Soper's itineraries and in the following list of species, I may call attention to the map of Northwest Territories published and issued by the Canadian Department of the Interior (1929).

The nomenclature and arrangement of species in the list of species follows. for Hepaticae, the recent work of Buch, Evans, and Verdoorn (1938), and for Musci, the classical work of Brotherus (1924-1925) in the second edition of Engler and Prantl's "Die Natürlichen Pflanzenfamilien."

I should like to express my indebtedness to Dr. Margaret Fulford, who aided in the identification of the Hepaticae, and to Dr. A. LeRoy Andrews, who named most of the species of *Sphagnum*, *Bryum* and *Pohlia*.

Hepaticae

PTILIDIACEAE

Ptilidium ciliare (L.) Nees. BAFFIN ISLAND: Cape Dorset. Hudson Strait. June 8, 1926. Soper 671c (Canad. Herb. 891); Pangnirtung Fiord. Cumberland Sound. July 26, 1924. Soper 71e, 72e (Canad. Herb. 855); Camp Kungovik. Lat. $65^{\circ} 35' N.$. July 10, 1929. Soper 11c, 16b, July 18, 1929. Soper 60a, 62b.

LEPIDOZIOACEAE

Blepharostoma trichophyllum (L.) Dumort. BAFFIN ISLAND: Amadjuak Bay. Hudson Strait. August 2, 1926. Soper 894 (Canad. Herb. 892).

EPIGONIANTHACEAE

Barbilophozia Hatcheri (Evans) Loeske (*Lophozia Hatcheri* Evans). BAFFIN ISLAND: Cape Dorset, Hudson Strait. June 8, 1926. Soper 671b (Canad. Herb. 891). July 25, 1926. Soper 839c (Canad. Herb. 900).

Gymnocola inflata (Huds.) Dumort. BAFFIN ISLAND: Kingua Fiord, Cumberland Sound, August 3, 1924, Soper 156b (Canad. Herb. 836); Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379e (Canad. Herb. 879).

Lophozia alpestris (Schleich.) Evans. BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, August 13, 1924, Soper 196 (Canad. Herb. 849).

Orthocaulis Kunzeanus (Hüb.) Buch (*Lophozia Kunzeana* Evans). Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 16c.

Sphenolobus minutus (Crantz) Steph. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 894d (Canad. Herb. 892).

Temnoma setiforme (Ehrh.) Howe. BAFFIN ISLAND: Kingua Fiord, Cumberland Sound, August 1, 1924, Soper 120-121 (Canad. Herb. 854), 123b (Canad. Herb. 853), 124 (Canad. Herb. 852). Listed as *Chandonanthus setiformis* Lindb. in the first paper of this series (Steere, 1938).

Tritomaria quinquedentata (Huds.) Buch (*Lophozia quinquedentata* Cogn.). BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, July 26, 1924, Soper 71-72d (Canad. Herb. 855).

MARCHANTIACEAE

Marchantia polymorpha L. BAFFIN ISLAND: Amadjuak Bay, August 2, 1926, Soper 898 (Canad. Herb. 902). Both antheridiophores and archegoniophores are present on this material.

Musci

SPHAGNACEAE

Sphagnum teres (Schimp.) Angstr. BAFFIN ISLAND: Kingua Fiord, Cumberland Sound, August 1, 1924, Soper 120-121 (Canad. Herb. 854); Pangnirtung Fiord, Cumberland Sound, August 13, 1924, Soper 195-196 (Canad. Herb. 849).

Sphagnum Lindbergii Schimp. BAFFIN ISLAND: Kingua Fiord, Cumberland Sound, August 3, 1924, Soper 156 (Canad. Herb. 836), 157 (Canad. Herb. 837), 157 (Canad. Herb. 838); Pangnirtung Fiord, August 13, 1924, Soper 197-198 (Canad. Herb. 850).

Sphagnum fimbriatum Wils. BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, September 15, 1923, Soper 636 (Canad. Herb. 885).

Sphagnum Girgensohnii Russow. LABRADOR: Cape Mikkovik, September 22, 1926, Soper (Canad. Herb. 843). BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, September 15, 1923, Soper 640 (Canad. Herb. 883).

Sphagnum capillaceum (Weiss) Schrank, var. *tenellum* (Schimp.) Andrews. BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, September 15, 1923, Soper 637a (Canad. Herb. 884), July 26, 1924, Soper 71-72 (Canad. Herb. 855); Kingua Fiord, Cumberland Sound, August 2, 1924, Soper 147-148 (Canad. Herb. 851); Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 894a (Canad. Herb. 892); Fox Island, Nettilling Lake, August 24, 1925, Soper 627a (Canad. Herb. 840).

DITRICHACEAE

Ditrichum flexicaule (Schleich.) Hampe. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 11, 1926, Soper 676b (Canad. Herb. 896); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 17e, 19c; Koukdiuk River, August 31, 1925, Soper 698c (Canad. Herb. 844), 699 (Canad. Herb. 846); Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379k (Canad. Herb. 878). NORTH DEVON ISLAND: Beechey Island, August 17, 1923, Soper 318a (Canad. Herb. 875).

Ceratodon purpureus (Hedw.) Brid. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 3, 1926, Soper 903a (c. fr.) (Canad. Herb. 897); Blacklead Island, Cumberland Sound, August 23, 1924, Soper 298 (Canad. Herb. 830).

Distichium capillaceum (Sw.) Bry. eur. BAFFIN ISLAND: Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379g (Canad. Herb. 878), 380d (Canad. Herb. 877). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 294f (Canad. Herb. 872); Beechey Island, August 17, 1923, Soper 318d (Canad. Herb. 875).

DICRANACEAE

Dicranum elongatum Schleich. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 668c (Canad. Herb. 898). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 298c (Canad. Herb. 874).

Dicranum fuscescens Turn. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 14, 15d, 16a.

ENCALYPTACEAE

Encalypta streptocarpa Hedw. BAFFIN ISLAND: Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 380e (Canad. Herb. 877).

POTTIACEAE

Didymodon recurvirostris (Hedw.) Jennings (*D. rubellus* Mitt.). BAFFIN ISLAND: Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379m (Canad. Herb. 878).

Tortula ruralis (Hedw.) Smith. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 11, 1926, Soper 676c (Canad. Herb. 896); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 15b. NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 291d (Canad. Herb. 871), 294d (Canad. Herb. 872).

GRIMMIACEAE

Racomitrium sudeticum (Funck) Bryol. eur. NORTH DEVON ISLAND: Beechey Island, August 17, 1923, Soper 321 (Canad. Herb. 876).

Racomitrium lanuginosum (Hedw.) Brid. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 895 (Canad. Herb. 893); Blacklead Island, Cumberland Sound, August 23, 1924, Soper 299 (Canad. Herb. 831); Kingua Fiord, Cumberland Sound, August 1, 1924, Soper 123a (Canad. Herb. 853); Pangnirtung Fiord, September 15, 1923, Soper 635 (Canad. Herb. 886), July 26, 1924, Soper 68-70 (Canad. Herb. 856); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 11a, 15f, 16e. ELLESMERE ISLAND: Craig Harbour, June 25, 1923, B.C. Jakeman and L. F. Fielder (Canad. Herb. 866 and 858), August 12, 1923, Soper 251 (Canad. Herb. 860), 252c (Canad. Herb. 864).

In a manuscript note accompanying the collections from Camp Kungovik, Soper says of this species: "Common and in places abundant on granite uplands. This is the characteristic moss of granite areas and surpasses in abundance any other species. It covers, however, a relatively small area."

Racomitrium canescens (Hedw.) Brid. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 15.

BRYACEAE

Pohlia Wahlenbergii (Web. & Mohr) Andrews (*Mniobryum albicans* Limpr.). BAFFIN ISLAND: Cape Dorset, Hudson Strait, July 25, 1926, Soper 840 (Canad. Herb. 907), 846 (Canad. Herb. 899).

Pohlia cruda (L.) Lindb. BAFFIN ISLAND: Cape Dorset, Hudson Strait, August 15, 1923, Soper 663c (Canad. Herb. 905); Koollee River, Pangnirtung Fiord, Cumberland Sound, August 7, 1924, Soper 171 (Canad. Herb. 835). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 291c (Canad. Herb. 871), 294c (Canad. Herb. 872), 298 (Canad. Herb. 873).

Leptobryum pyriforme (Hedw.) Schimp. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 3, 1926, Soper 903b (Canad. Herb. 897).

Bryum obtusifolium Lindb. BAFFIN ISLAND: Cape Dorset, Hudson Strait, August 15, 1923, Soper 665a (Canad. Herb. 908); Wm. Fox Islands, Gordon Bay, Hudson Strait, June 28, 1926, Soper 751 (Canad. Herb. 895).

MNIACEAE

Mnium orthorrhynchium Brid. NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 298c (Canad. Herb. 873).

Mnium affine Bland. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 16g.

Cinclidium subrotundum Lindb. BAFFIN ISLAND: Cape Dorset, Hudson Strait, July 25, 1926, Soper 845 (Canad. Herb. 888).

Cinclidium arcticum (Bry. eur.) C. Müll. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 19d, July 18, 1929, Soper 62a, "A moss occurring in very wet situations around ponds and streams"; Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379d (Canad. Herb. 878, 879), 380c (Canad. Herb. 877).

Cinclidium hymenophyllum (Bryol. eur.) Lindb. NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 294g (Canad. Herb. 872).

AULACOMNIACEAE

Aulacomnium palustre (Hedw.) Schwaegr. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 663b (Canad. Herb. 905), 664 (Canad. Herb. 890), 668b (Canad. Herb. 898); Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 894f (Canad. Herb. 892); Camp Kungovik, Lat. 65° 35' N., July 18, 1929, Soper 60d.

Aulacomnium acuminatum (Lindb. & Arn.) Paris. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 17a. Mr. Soper says of this plant, in his notes: "This species is the most common of the mosses of the lowlands and open tundras. In places it covers the entire ground, though normally it contributes very largely to the formation of typical tundra hummocks, or 'nigger-heads.'" Although this species was reported from Ellesmere Island by Bryhn (1906), it is not included in the most recent revision of the North American species of *Aulacomnium* (Sayre, 1935), even as a synonym.

Aulacomnium turgidum (Wahlenb.) Schwaegr. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 663a (Canad. Herb. 905), 668a (Canad. Herb. 898); Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 893 (Canad. Herb. 901); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 13a, 15e; Fox Island, Nettilling Lake, August 24, 1925, Soper 627b (Canad. Herb. 840), 628a (Canad. Herb. 841), 629c (Canad. Herb. 842); Koukdjuak River, August 31, 1925, Soper 698a (Canad. Herb. 844); Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379a (Canad. Herb. 878, 879). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 298a (Canad. Herb. 873).

MEESEACEAE

Meesea uliginosa Hedw. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 894e (Canad. Herb. 892); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 17g.

CATOSCOPIACEAE

Catoscopium nigrum (Hedw.) Brid. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 192. Mr. Soper says, in his manuscript notes: "A moss of occasional occurrence on the open tundra where it tends to develop isolated hummocks of small extent." This moss is usually sterile in the Arctic, and upon first study is extremely puzzling because, for the first year, at least, the innovations are usually decidedly tristichous, with very small leaves, although the areolation is entirely normal. As a result of its abnormal macroscopic appearance, this Arctic form has been reported by more than one author as a species of *Seligeria*.

BARTRAMIACEAE

Philonotis fontana (Hedw.) Brid. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 665e (Canad. Herb. 908); Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379h (Canad. Herb. 878).

Philonotis tomentella Mol. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 17b.

TIMMIACEAE

Timmia austriaca Hedw. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 11e, 17f; Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379i (Canad. Herb. 878). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 289 (Canad. Herb. 868), 289c (Canad. Herb. 870), 291b (Canad. Herb. 871), 294b (Canad. Herb. 872); Beechey Island, August 17, 1923, Soper 318e (Canad. Herb. 875).

ORTHOTRICHACEAE

Orthotrichum microblepharum Schimp. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 15i.

THELIACEAE

Myurella julacea (Schwaegr.) Bry. eur. BAFFIN ISLAND: Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379i (Canad. Herb. 878). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 294e (Canad. Herb. 872).

THUIDIACEAE

Abietinella abietina (Brid.) C. Müll. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 11d, 13b, 15a. Mr. Soper remarks that this is a "Moss occurring on granite uplands, sparingly distributed."

AMBLYSTEGIACEAE

Campyllum stellatum (Hedw.) Lang. & C. Jensen. BAFFIN ISLAND: Cape Dorset, June 6, 1926, Soper 665f (Canad. Herb. 908), June 11, 1926, Soper 677c (Canad. Herb. 903); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 17d, 19f; Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379c (Canad. Herb. 878, 879).

Drepanocladus revolvens (Sw.) Warnst. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 556b (Canad. Herb. 908); Pangnirtung Fiord, Cumberland Sound, September 15, 1923, Soper 637c (Canad. Herb. 884).

Drepanocladus uncinatus (Hedw.) Warnst. BAFFIN ISLAND: Cape Dorset, Hudson Strait, July 25, 1926, Soper 839b (Canad. Herb. 900); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 13c, 15g; Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379l (Canad. Herb. 878). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 294a (Canad. Herb. 872). ELLESMERE ISLAND: Craig Harbour, August 12, 1923, Soper 252c (Canad. Herb. 863).

Drepanocladus intermedius (Lindb.) Warnst. BAFFIN ISLAND: Cape Dorset, June 11, 1926, Soper 677b (Canad. Herb. 903); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 18a "A moss of general distribution on the tundra, where it occupies very wet situations," June 18, 1929, Soper 61b.

Drepanocladus exannulatus (Gümb.) Warnst. BAFFIN ISLAND: Kingua Fiord, Cumberland Sound, August 1, 1924, Soper 126 (Canad. Herb. 839); Pangnirtung Fiord, Cumberland Sound, August 4, 1924, Soper 179 (Canad. Herb. 857).

Drepanocladus fluitans (Hedw.) Warnst. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 892 (Canad. Herb. 889).

Drepanocladus aduncus (Hedw.) Mönkem. NORTH DEVON ISLAND: Beechey Island, August 17, 1923, Soper 318b (Canad. Herb. 875).

Drepanocladus aduncus (Hedw.) Mönkem. var. *polycarpus* (Bland.) Warnst. BAFFIN ISLAND: Blacklead Island, Cumberland Sound, August 25, 1924, Soper 317 (Canad. Herb. 829).

Drepanocladus badius (Hartm.) Roth. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 894b (Canad. Herb. 892); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 19b; Koukdjuak River, August 31, 1925, Soper 699 (Canad. Herb. 846).

Drepanocladus brevifolius (Lindb.) Warnst. BAFFIN ISLAND: Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 380b (Canad. Herb. 877).

Calliergon turgescens (Th. Jensen) Kindb. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 11, 1926, Soper 676 (Canad. Herb. 896); Camp Kungovik, Lat. 65° 35' N., July 10, 1929.

Calliergon giganteum (Schimp.) Kindb. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 18, "A moss of general distribution on the tundra where it occupies very wet situations," July 18, 1929, Soper 60b, "A moss observed commonly in very wet situations," 61a, "A moss observed only in submerged ground on the margin of streams."

Calliergon sarmentosum (Wahlenb.) Kindb. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 665d (Canad. Herb. 908).

Calliergon cordifolium (Hedw.) Kindb. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 666b (Canad. Herb. 894).

Calliergon stramineum (Brid.) Kindb. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 666c (Canad. Herb. 894); Pangnirtung Fiord, Cumberland Sound, September 15, 1923, Soper 637b (Canad. Herb. 884), July 26, 1924, Soper 71-72c (Canad. Herb. 855), August 13, 1924, Soper 195-196, in part (Canad. Herb. 849).

Scorpidium scorvioides (Hedw.) Limp. BAFFIN ISLAND: Amadjuak Bay, Hudson Strait, August 2, 1926, Soper 892a (Canad. Herb. 889).

BRACHYTHECIACEAE

Tomenthypnum nitens (Hedw.) Loeske. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 12, "Moss of granite areas, relatively common," 17h, July 18, 1929, Soper 60c; Fox Islands, Nettilling Lake, August 24, 1925, Soper 627c (Canad. Herb. 840), 628b (Canad. Herb. 841), 629b (Canad. Herb. 842); Koukdjuak River, August 31, 1925, Soper 650b (Canad. Herb. 845); Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379b (Canad. Herb. 879).

Brachythecium albicans (Hedw.) Bry. eur. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 17c, July 18, 1929, Soper 61c; Fox Islands, Nettilling Lake, August 24, 1925, Soper 628c (Canad. Herb. 841).

Brachythecium salebrosum (Hoffm.) Bry. eur. BAFFIN ISLAND: Koukdjuak River, August 31, 1925, Soper 698d (Canad. Herb. 844).

ENTODONTACEAE

Orthothecium intricatum (Hartm.) Bryol. eur. BAFFIN ISLAND: Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 19g.

Orthothecium chryseum (Schwaegr.) Bryol. eur. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 11, 1926, 677a (Canad. Herb. 903); Camp Kungovik, Lat. 65° 35' N., July 18, 1929, Soper 60e, 62c; Koukdjuak River, August 31, 1925, Soper 698b (Canad. Herb. 844); Pond Inlet, September 2, 1923, Soper 518 (Canad. Herb. 881); Strathcona Sound, Admiralty Inlet, August 19, 1923, Soper 379f (Canad. Herb. 878), 380a (Canad. Herb. 877). NORTH DEVON ISLAND: Beechey Island, August 17, 1923, Soper 318c (Canad. Herb. 875).

HYPNACEAE

Hypnum cupressiforme Hedw. NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 289f (Canad. Herb. 689), 298 (Canad. Herb. 873).

Hypnum callichroum Brid. BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, September 18, 1923, Soper 648 (Canad. Herb. 887).

RHYTIDIACEAE

Rhytidium rugosum (Hedw.) Kindb. BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, August 13, 1924, Soper 194 (Canad. Herb. 833).

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) Bryol. eur. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 668e (Canad. Herb. 898); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 11b, 13d, 15h, 16f, "Moss occurring on granite uplands; sparingly distributed"; Pangnirtung Fiord, Cumberland Sound, July 26, 1924, Soper 71b-72b (Canad. Herb. 855); Fox Islands, Nettilling Lake, August 24, 1925, Soper 629a (Canad. Herb. 842); Koukdjuak River, August 31, 1925, Soper 650a (Canad. Herb. 845).

POLYTRICHACEAE

Polytrichum alpinum Hedw. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 665c (Canad. Herb. 908), June 8, 1926, Soper 671a (Canad. Herb. 891), July 25, 1926, Soper 839a (Canad. Herb. 900). NORTH DEVON ISLAND: Dundas Harbour, August 15, 1923, Soper 289a (Canad. Herb. 868), 291a (Canad. Herb. 871).

Polytrichum juniperinum Hedw. BAFFIN ISLAND: Cape Dorset, Hudson Strait, June 6, 1926, Soper 668f (Canad. Herb. 898); Camp Kungovik, Lat. 65° 35' N., July 10, 1929, Soper 16d; Blacklead Island, Cumberland Sound, August 21, 1924, Soper 287 (Canad. Herb. 832). ELLESMERE ISLAND: Craig Harbour, August 12, 1923, Soper 252d (Canad. Herb. 865).

Polytrichum strictum Banks. BAFFIN ISLAND: Pangnirtung Fiord, Cumberland Sound, August 13, 1924, Soper 197-198, in part (Canad. Herb. 850), 199 (Canad. Herb. 834).

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Actinocheita¹

Fred A. Barkley and Merton J. Reed

The publication of the combination *Actinocheita potentillifolia* (Turcz.) Bullock² requires further comment.

While specimens of the Mociño and Sessé collection are available on loan from the Madrid Herbarium at Field Museum Herbarium for most of the plants illustrated in A. De Candolle's *Calque des Dessins de la Flora du Mexique, de Mociño et Sessé* and for the plants described in Sessé and Mociño's *Plantae Novae Hispaniae*, there are unfortunately no specimens available for the plants illustrated in plate 189 of the former work, nor are there any called "Tetlazier," so that the interpretation of the description of *Rhus Filicina* DC. and plate 189 in the *Calques* (on which the De Candolle description of this species is undoubtedly based), must rest on what is available in the description and illustration when compared to known specimens from the general region of their collection (southern Mexico). This of necessity means that there will always be room for a possible misinterpretation of them as of all illustrations and descriptions with which no specimens are definitely associated.

When the senior author made the statement³ that there might be some uncertainty about the interpretation of the original De Candolle description and plate as *Actinocheita filicina* he did not imply that there was any possibility that they could be interpreted as applying to *Bursera bipinnata* (Sessé et Moc. ex DC.) Engl., for if one takes the illustration of this plant (Pl.1) and the original description:⁴

§. 1. *Foliis impari-pinnatis.*

3. *R. FILICINA* (fl. mex. ic. ined.) foliis 7-9-jugis, petiolo nudo, foliolis sessilibus pinnatifidis pilosis oblongis, lobis obtusis pilo aristatis. ♀ in Mexici montibus. Ex fl. mex. mss. dicitur *Tetlazier* sed non est Tetlazier
Hern. mex. 153. Fructus pilis violaceis hirtus.

[3. *R. FILICINA* (Flora of Mexico Illustrations, unpublished) leaves with 15-19 leaflets, petiole non-alate, leaflets sessile, oblong, pilose, pinnately cleft, lobes obtuse, pilose-aristate. Tree in the Mexican Mountains. From the [unpublished] Flora of Mexico manuscript [of Sessé and Mociño fide Sprague in Kew Bull. Misc. Inf. 1926, pp. 417-425] called *Tetlazier* but is not Tetlazier of F. Hernandez', *Rerum medicarum Novae Hispaniae thesaurus*.... p. 153. 1651. Fruit pilose with violet hairs.]

one cannot but wonder that anyone might seriously suggest either that the

¹ This work, in part, made possible through a grant from the Penrose fund of the American Philosophical Society.

² Bullock. Kew Bull. Misc. Inf. 1937, p. 441.

³ Barkley. Ann. Mo. Bot. Gard. 24:3, 1936, in footnote.

⁴ De Candolle, A. P. *Prodromus Systematis Naturalis Regni Vegetabilis*, 1825, p. 67.



Fig. 1. Known area of distribution of *Actinocheita filicina* (DC.) Barkley. (Illustration furnished through the courtesy of the Missouri Botanical Garden.)

description (even excluding the statement in reference to the fruit) or illustration as referring to *Bursera bipinnata* when compared to a series of specimens of that species. The carefully drawn portions of the original illustration which is now available from a photograph of it in the Field Museum of Natural History (Pl. 1) shows a very pilose apical portion to a staghorn-like branch, a once pinnate leaf with a nude rachis, crenate-serrate and bristly-aristate, sessile leaflets characteristic of the plant Turczaninow described as *Rhus potentillaefolia*, not a slender glabrous branch bearing bipinnate leaves with more or less alate rachi, with leaflets remote and very sparsely pilose as one finds in *B. bipinnata*.

When the statement was made that there might be some doubt⁵ in the interpretation of this De Candolle plate it was with the idea in mind that there are several plants of similar appearance and the fact that descriptions and drawings are never in themselves sufficiently complete to be absolutely reliable without associated specimens, however it did not mean that there is any reasonable doubt concerning their identity in this case.

The interpretation of *Rhus Filicina* as being conspecific with *Rhus potentillaefolia* is based on the interpretation of plate 189 of *Calque des Dessins* . . . primarily, the plate which Mr. Bullock states undoubtedly served as the basis for De Candolle's description of *R. Filicina*. The original drawing with the

⁵ Barkley, *ibid.*

carefully drawn portion (Pl. 1) makes the former suggestion proposed after study of the blue-print⁶ almost a certainty and removes all possible doubt as to its misinterpretation as *B. bipinnata*.

Apparently plate 217 of *Calque des Dessins* . . . is no longer in existence for the recent complete set of photographs of the original De Candolle drawings of the Mociño and Sessé plants now available at the Field Museum of Natural History does not contain a reproduction of this plate. From the description of *R. Tetlatziam* in *Plantae Novae Hispaniae* it undoubtedly referred to the same species, a supposition made more probable by De Candolle's reference to the name "Tetlatzian" with his description. The interpretation of the description and plate does not, however, rest on the reference to "dicitur Tetlatzian sed non est Tetlacian Hern. Mex. 153" nor "Fructus pilis violaceis hirtus" as Mr. Bullock presumed, but they certainly do not detract from such an interpretation.

While the author had in mind the biological entity including *Rhus potentillaefolia* Turcz. in the creation of the genus *Actinocheita*, it is necessary to point out that the type of the genotype is plate 189 of A. De Candolle's *Calque des Dessins*. . . (not specimens of *Rhus potentillaefolia* Turcz. as has been erroneously assumed) so that if plate 189 of the *Calque*. . . were to be proven other than conspecific with *Rhus potentillaefolia* (and there has been no adequate evidence produced to so prove) then the type of the genus would have been removed so that it would seem a new name for the genus would have then been indicated⁷ rather than a new combination under the old genus name.

The following brings data concerning the genus to date:

ACTINOCHAITA Barkley

ACTINOCHAITA Barkl., Ann. Mo. Bot. Gard. 24:2. 1937; *ibid.* 310; Bullock, Kew Bull. Misc. Inf. 1937, 441.

Rhus DC., Prodr. 2:67. 1825, in part; Turcz., Bull. Soc. Nat. Moscou 31:469. 1858, in part; A. DC., Calq. Dess. Fl. Mex. Moc. & Sessé, t. 189. 1874, in part; Hemsl., Biol. Cent.-Am. Bot. 1:217, 218. 1880, in part; Engler in DC., Monogr. Phaner. 4:383. 1883, in part; Sessé & Moc., Pl. Nov. Esp., p. 47. 1887, in part; ed. 2, p. 44. 1893, in part; Standl., Contr. U. S. Nat. Herb. [Trees & Shrubs Mex.] 23:665. 1923, in part.

Toxicodendron Kuntze, Rev. Gen. Pl., pt. 1, p. 153. 1891, in part.

Deciduous trees with few staghorn-like, ash-gray branches. Leaves alternate, imparipinnate, more or less persistent, clustered near the apex of the branches; leaflets many, densely pubescent, rugose; rachis not winged. Bracts of the inflorescence lanceolate, deciduous. Flowers polygamo-dioecious, in ascending panicles in the axils of the leaves, appearing with the leaves. Petals and sepals 5, spreading. Ovary 1-celled, raised upon a column formed by the

⁶ Barkley, *ibid.*, pl. 1.

⁷ International Rules of Botanical Nomenclature, Art. 18.

disk and partly adherent to it; style 3-branched, terminal. Drupe almost symmetrical, clothed with long, soft, reddish hairs.

A single species is known:

ACTINOCHEITA FILICINA (DC.) Barkl., Ann. Mo. Bot. Gard. 24: 2. 1937.

Rhus Filicina DC., Prodr. 2:67. 1825; A. DC., Calq. Dess. Fl. Mex. Moc. & Sessé, pl. 189. 1874; Hemsl., Biol. Cent.-Am. Bot. 1:217. 1880.

R. potentillaefolia Turcz., Bull. Soc. Nat. Moscou 31:469. 1858; Hemsl., Biol. Cent.-Am. Bot. 1:218. 1880; *ibid.* 4:21. 1886, in note; Engler in DC., Monogr. Phaner. 4:383. 1883; Standl., Contr. U. S. Nat. Herb. [Trees & Shrubs Mex.] 23:669. 1923.

R. Tetlatziam Sessé & Moc., Pl. Nov. Esp., p. 47. 1887; ed. 2, p. 44. 1893.

Actinocheita potentillifolia Bullock, Kew Bull. Misc. Inf. 1937, 441.

Barsera bipinnata (Schlecht.) Engler in DC., Monogr. Phaner. 4:49. 1883, in part, as to *Rhus filicina* in syn.; Hemsl., Biol. Cent.-Am. Bot. 4:19. 1886, in part, as to *Rhus filicina* in syn.; Bullock, Kew Bull. Misc. Inf. 1936, 355, as to *Rhus filicina* in syn.

Toxicodendron potentillifolium O. Kuntze, Rev. Gen. Pl., pt. I, p. 154. 1891.

Shrubs and small trees to 5 m. in height, with few staghorn-like branches covered with tuberculate leaf scars; branches ash-gray, glabrous below and densely pubescent at the apex, nude at base and clothed heavily near the summit with leaves; leaves alternate, rugose, imparipinnate, 9-33 cm. long, deciduous; leaflets 13-29, sessile, broadly linear, to 6 cm. long, sometimes as small as 0.5 cm., hoary-tomentose, lighter below, with revolute margins, lobes crenate, usually cristate-pointed, apex more or less acute, base truncate; rachis naked, densely pubescent; flowers polygamo-dioecious, disposed in ascending panicles half as long as the subtending leaves and appearing with them; bracts linear to subrotund, persistent, pilose-hirsute; sepals 5, deltoid-lanceolate, densely pubescent; stamens with thickened filaments longer than the ovoid anthers; pistil with 3 short styles, ovary on a torus formed by the disk, 1-celled, ovule anatropous; drupe almost symmetrical, villous, clothed with long, soft, violet-red hairs.

Type: In all probability the original material on which this species was founded no longer exists; but the species is based primarily on plate 189 of *Calque des Dessins de la Flora du Mexique, de Mocino et Sessé*, 1874, and is typified by Pringle 4572 which is represented in the larger herbaria of America and Europe.

MEXICO: coll. of 1791, *Thaddaeus Haenke* 1503 (Field Mus.); *Jurgensen* 283 (Kew Herb.S)

⁸ The authors are indebted to Sir Arthur Hill and the Royal Botanic Gardens at Kew, England for photographs of these specimens for their study.



PLATE 1: *Actinocheila flicina* (DC.) Barkley

Photograph of the original drawing from which the tracing for plate 189 of A. De Candolle's *Calques des Dessins, Flora du Mexique, de Mocino et Sessé* was made (see pl. 3, fig. 2, insert). This plate is listed in the "Enumeration d'après l'ordre des numéros" as "*Rhus flicina* 2. p. 67." As it is probable that the original material on which the species was founded no longer exists, *Actinocheila flicina* must rest on this drawing.

In no place in the carefully drawn portion of the specimen are the leaves shown

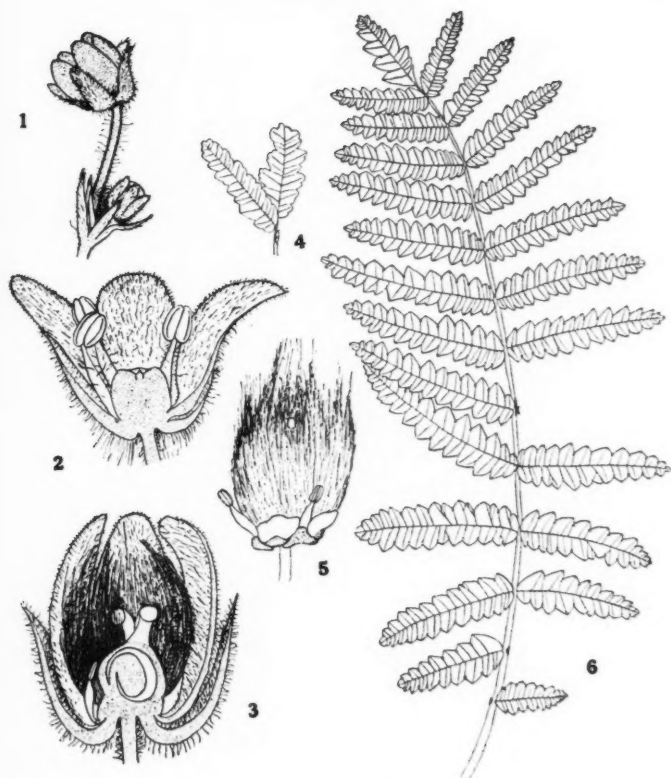


PLATE 2: Fig. 1, Flower, x 6, from *Pringle 9164*; Fig. 2, Longitudinal section through a staminate flower, x 14, from *Purpus 1236*; Fig. 3, Longitudinal section through pistillate flower, x14, from *Pringle 4752*; Fig. 4, Terminal portion of a leaf, x.7, from *Pringle 4752*; Fig. 5, Pistillate flower with petals and sepals removed, x14, from *Pringle 4752*; Fig. 6, Leaf, x.7, from *Pringle 9164*.

as bipinnate, and in *only* one place in the hurriedly drawn portion is it so shown. When one considers the rush in which these drawings were executed one can understand such inaccuracies in drawing, so that the authors feel that what at first glance appear to be leaflets of a bipinnately compound leaf are attempts of a hurried and not too skilled artist to show the veins which occur at the lobes and sinuses of the leaflets of the species under consideration, which at the stage of development of the leaves here shown certainly often look in pressed specimens bipinnate until observed carefully. (See Pls. 3 Fig. 2, 2 figs. 4 & 6, 4, & 5). Certainly the description De Candolle drew from this plate does not describe bipinnate leaves, and he had seen the specimen!

(Photograph furnished through the courtesy of the Field Museum of Natural History.)

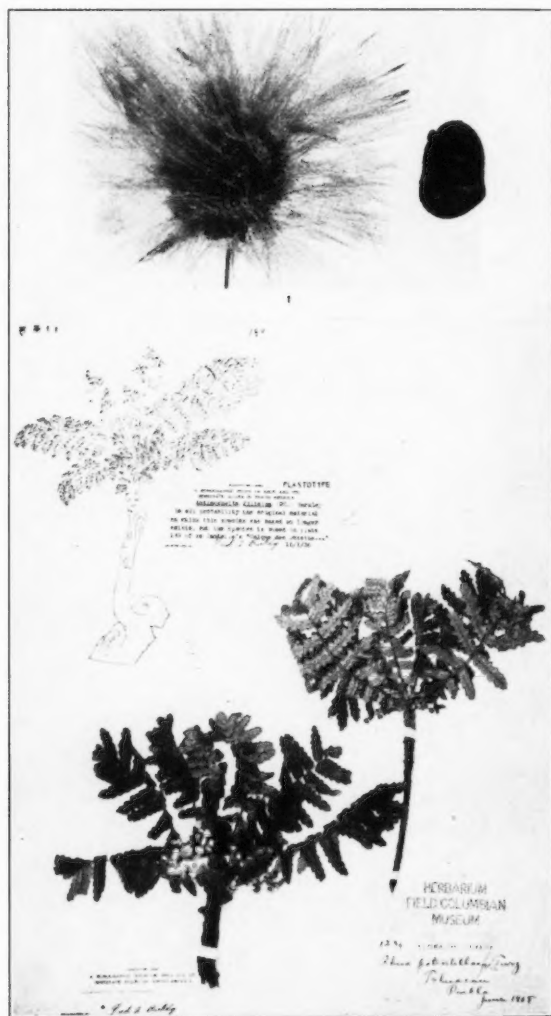


PLATE 3: *Actinocheita filicina* (DC.) Barkley; Fig. 1, Fruit and seed, x 4.1, from Seler 1419. Note the long pilosity of the fruit-coat and the rugosity of the seed; Fig. 2, From specimen, Purpus 1236, in Field Museum Herbarium. The insert at the upper left is a reproduction of plate 189 from de Candolle's *Calque des Dessins*...



PLATE 4: *Actinocheita filicina* (DC.) Barkley; from specimen collected by C. G. Pringle 4752, on limestone ledges, in Tomellin Canyon, Oaxaca, Mexico, altitude 2,500 ft., July 31, 1894; this specimen is typical of the species. (Illustration furnished through the courtesy of the Missouri Botanical Garden.)



PLATE 5: *Actinocheita filicina* (DC.) Barkley; The specimen on the right was collected by Galeotti 4006A, from Cordillera, Oaxaca, August 1840, and represents the type collection of *Rhus potentillaefolia* Turcz. (Photograph furnished through the courtesy of Sir Arthur Hill and the Royal Botanic Gardens, Kew, England.)

GUERRERO: Acuitlapan, 1900 m., Oct. 1935, *Mrs. Gordon Abbott 11* (Gray Herb.); shrub 10 to 15 feet, mountains above Iguala, Oct. 4, 1900, *C. G. Pringle 9164* (Mo. Bot. Gard., Field Mus., U. S. Nat. Herb., Gray Herb.).

OAXACA: Cañon del Tomellin, Estacion de Almoloyas, Sept. 29, 1907, *C. Conzatti 2019* (Field Mus., N. Y. Bot. Gard.); District of Nochixtlan, Cuesta de Henaudilla, *C. Conzatti 4247* (U. S. Nat. Herb.); Cordillera, Aug. 1840, *Galeotti 4006A* (cotype of *Rhus potentillaeifolia*, Kew. Herb.8); Cuesta de Nochixtlan, 2000 m., May, 1899, *V. Gonzalez & C. Conzatti 937* (Gray Herb.); six miles above Dominguillo, Oct. 3, 1893, *E. W. Nelson 1593* (U. S. Nat. Herb.); six miles above Dominguillo, Oct. 20, 1894, *E. W. Nelson 1825* (N. Y. Bot. Gard., U. S. Nat. Herb., Gray Herb.); limestone ledges, Tomellin Cañon, July 31, 1894, *C. G. Pringle 4752* (Mo. Bot. Gard., Field Mus., N. Y. Bot. Gard., Brooklyn Bot. Gard., Phila. Acad. Nat. Sci., U. S. Nat. Herb. Univ. Cal., Gray Herb.); Nov. 27, 1895, *Caec. & Ed. Seler 1419* (N. Y. Bot. Gard., Gray Herb.); Rio Seco, Necaltepec, alt. 3100 ft., "Poison to the touch," Sept. 21, 1895, *Rev. Lucius C. Smith 777* (Gray Herb.).

PUEBLA: Tehuacan, June, 1905, *C. A. Purpus 1236* (Mo. Bot. Gard., Field Mus., N. Y. Bot. Gard., Univ. Cal., Gray Herb.); Tlacuiloltepec, May, 1909, *C. A. Purpus 4065 (in part)* (Mo. Bot. Gard., N. Y. Bot. Gard., Field Mus., Gray Herb.); Tehuacan, Sept., 1911, *C. A. Purpus 5702* (Mo. Bot. Gard., Univ. Cal.); Tehuacan, Aug., 1905, *J. N. Rose, Walter Hough & J. H. Painter 9967* (N. Y. Bot. Gard., U. S. Nat. Herb., Gray Herb.).

DEPARTMENT OF BOTANY,
MONTANA STATE UNIVERSITY,
MISSOULA, MONTANA.

A Phytosociological Study of a Cypress-gum Swamp in Southeastern Louisiana

Thomas F. Hall* and William T. Penfound**

Introduction

Ecologists are always interested in studying virgin stands of rapidly vanishing communities which are being destroyed by man. Such a stand was investigated in the Pearl River Valley in the southeastern part of St. Tammany Parish, Louisiana (Figs. 1 and 6). This swamp has not been subjected to drainage and at the beginning of the study no evidence of cutting was present. There appears to be no immediate danger of the area being cut over, due mainly to its youth, although active logging operations were renewed in the summer of 1937 near the town of Pearl River, Louisiana.

The swamp lies on the tract of land which was proposed as the Honey Island National Park (Viosca, '33). The present study includes not only a phytosociological analysis of the community but also records of certain edaphic factors. Approximately fifty trips were made to the swamp from the spring of 1936 to the summer of 1937. In addition to the routine trips the following places were visited during the period of the study: (1) a drained cypress-gum swamp in Jefferson Parish which was studied by O'Neill in 1931, (2) an undrained, cut-over cypress-gum swamp near Raceland, La., (3) a pond cypress-slash pine swamp near Mandeville, La., (4) old, primeval cypress-gum and pure gum swamps in the Pearl River Valley, and (5) young swamps in the lower deltas of the Pearl and the Mississippi Rivers.

Historical

The Acolapissa Indians formerly inhabited the lower part of the valley and called the Pearl River "Talcatcha," which in their native tongue, means Rock River. If present conditions are indicative of the recent past, it seems probable that the River was so designated by the Indians in recognition of the gravel beds which are found in its lower reaches.

The "Talcatcha" when first visited by white man was called the "River of the Acopalissa," after the Indian Settlement which was found about four leagues north of the mouth. About 1702, some pearls were found in the river which attracted Iberville's attention. Subsequently the "River of Acolapissa" or "Talcatcha" was known as the Pearl River as a result of this circumstance (Swanton, '11).

Indian Village, which is situated on the west bank of the West Pearl

* I.von High School, Covington, La.

** Tulane University, New Orleans, La.

River approximately ten miles from its mouth, is represented at present only by burial mounds. These mounds, from three to six feet high, are composed mainly of the tests of the brackish water clam and cover an area of several hundred square yards. Since they are in a fresh water area and contain fragments of pottery, arrowheads, and human skeletons, there is no doubt as to their origin. In the light of these facts, the area is still known as Indian Village.

The Region

The area studied is located within the deltaic limits of the Pearl River Valley (Fig. 1). The Pearl River system has its source in east central Mississippi, flows southward through that state, continues into the southeastern part of Louisiana and finally empties into the Rigolets Pass and the Mississippi Sound. In the southeastern part of St. Tammany Parish the Pearl River system becomes a complex braided stream. The greater number of branches

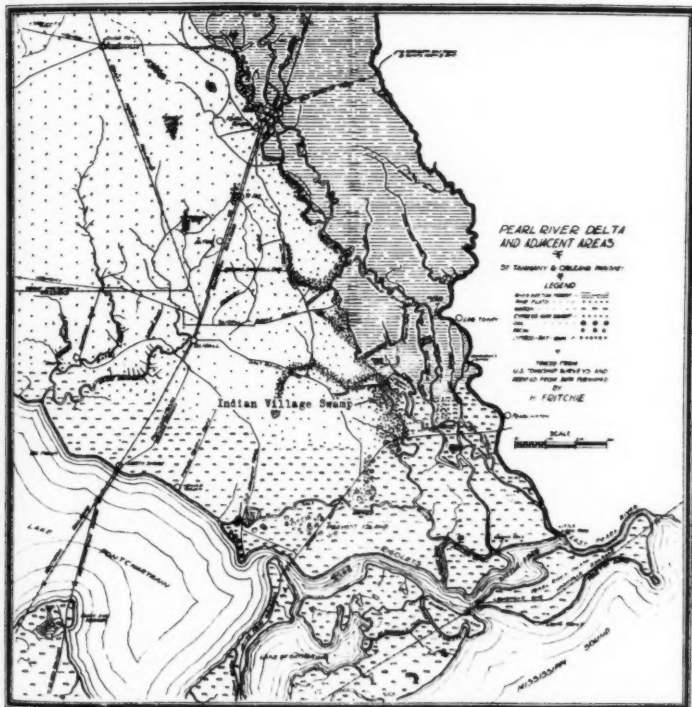


Fig. 1. Pearl River Delta and adjacent areas.

is to be found in the upper valley which cuts through the elevated Gulf Coastal Plain.

The flood plain of the Pearl River system, in its lower reaches, may be divided into two parts; namely, (1) the restricted flood plain, and (2) the unrestricted flood plain.

THE RESTRICTED FLOOD PLAIN

The restricted flood plain lies north of the short-cut of U. S. Highway Number 90 to the Gulf Coast, and the flood waters are confined between the elevated Gulf Coastal Plain of Louisiana on the west and that of Mississippi on the east. In this part of the Valley the waters are confined to the stream beds during the dry season, but spread over the valley during the late winter and early spring. During the months of January, February, and March, the water is ten feet deep in these swamps, and in the summer months, the water table may be three or four feet below the surface of the swamp floor. It is evident that the species which survive must be very tolerant to fluctuations in water level.

THE UNRESTRICTED FLOOD PLAIN

The unrestricted flood plain lies mainly to the south of the short-cut of U. S. Highway Number 90, and the flood waters of the system spread out over approximately fifty square miles of low marshland in this immediate locality. The marshlands represent the younger portion of the region and are

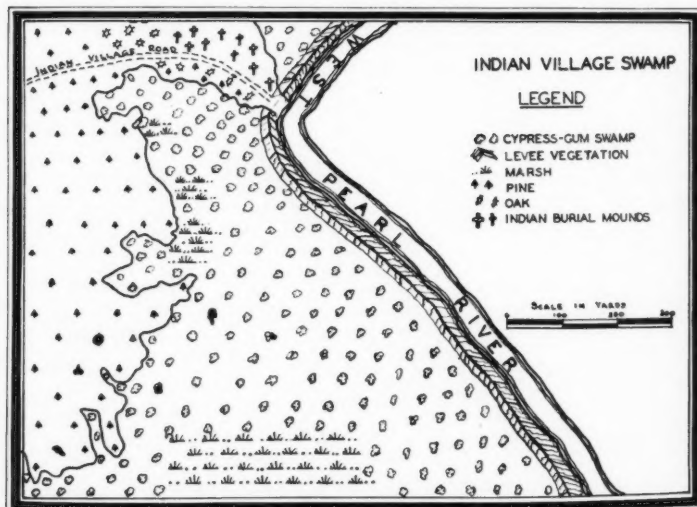


Fig. 2. Indian Village Swamp and Environs.

aggraded by the fluvial deposits of the Pearl River. The natural levees are formed by the deposition of the coarser sediments as the waters flood over the banks and the back lands are aggraded, but less rapidly, by the finer sediments.

The natural levees are approximately eighteen inches high in the upper parts of the unrestricted valley, but gradually diminish in height, and practically disappear as the debouchures are reached. These levees, when present, vary in width from a few feet to several hundred yards, and the type of vegetation which they support depends upon the degree of elevation above the mean ground water level.

Ridge	Swamp	Marsh
<i>Certhamnus ceriferus</i>	<i>Nyssa biflora</i>	<i>Mariscus jamaicensis</i>
<i>Quercus nigra</i>	<i>Taxodium distichum</i>	
<i>Sabal louisiana</i>	<i>Nyssa aquatica</i>	
<i>Taxodium distichum</i>	<i>Rufacer drummondii</i>	
<i>Nyssa biflora</i>		
<i>Nyssa aquatica</i>		
<i>Rufacer drummondii</i>		



Fig. 3. Sectional view of levee and backlands in fresh water region of the unrestricted flood plain, showing the relation of vegetation to the water level.

On the higher natural levees a fragmentary deciduous forest is found (Fig. 3). Behind these ridges and away from the river are found the cypress-gum swamps. In back of the latter usually extensive fresh water marshes are located which have saw-grass (*Mariscus jamaicensis*) as the dominant species (Fig. 3). Farther south in the unrestricted flood plain brackish conditions are encountered, and the saw-grass is replaced by the couch grass (*Spartina patens*) as the predominant marsh species.

Indian Village Swamp

On an east to west line, at Indian Village, the Pearl River Valley is approximately three miles wide, and is bordered on the east by the pinelands of Mississippi and on the west by similar lands of Louisiana. Here, there are seven main streams running through the valley, from east to west as follows: East Pearl River, Chalon Bayou, Morgan Bayou, East Middle River, West Middle River, Mill Bayou, and the West Pearl River (Fig. 1). Lying between the levees of any two adjacent streams are the so-called backlands which are approximately one and one-half to three feet below the crests of the levees. Such shallow backlands are occupied by cypress-gum communities.

The cypress-gum swamp investigated will be referred to in future as the Indian Village Swamp. This swamp is bounded on the north by the Indian

Village Road and burial mounds, on the east by the levee of the West Pearl River, on the south by a sawgrass marsh, and on the west by the pinelands of the Gulf Coastal Plain (Fig. 2). The average width of this swamp, in an east to west direction, is about three hundred yards; and the length from north to south is approximately one-half mile.

At Indian Village the levee of the West Pearl River has an elevation of approximately eighteen inches above the mean water level. Behind the levee, where the land is below mean water level, is the cypress-gum swamp. Closer to the pineland side of the swamp are three patches of marsh grasses, two being composed mainly of saw-grass (*Mariscus jamaicensis*) and the other of cut grass (*Zizaniopsis miliacea*) (Figs. 2 and 4). The patches of marsh



Fig. 4. A patch of marsh grass, near the west edge of the swamp, which is being invaded by the swamp species.

grasses occur where the water is deeper than in the swamp (Fig. 3). The larger trees of the swamp give way to smaller ones as the patches of marsh grasses are approached, and a graded series is found from the east and west edges of the swamp to the marsh patches. This sequence clearly indicates that the swamp is gradually invading and replacing the marshlands of this locality. This latter point is convincingly substantiated by the fact that partially decomposed marsh grasses, which have been buried by alluvial deposits, may be found from two to three feet below the surface of the swamp floor. Therefore, the Indian Village Swamp may be termed a fresh-water marsh-successional swamp.

The swamp trees are invading the backlands, formerly marshlands, more rapidly from the leveed edge westward than from the pinelands eastward; this is evident since the patches of marsh grasses are much closer to the pinelands

than to the levees (Fig. 2). The much greater rate of invasion from the levee side is not surprising since the Pearl River is the primary agent of sedimentation.

The differences in elevation of the surface of the swamp and marsh floors already have been noted and additional data were obtained on some of the physical and chemical characteristics of the soil, soil water, and surface water of the Indian Village Swamp. These data, which follow, are believed to be representative of the conditions as they exist in this swamp and the adjacent backlands.

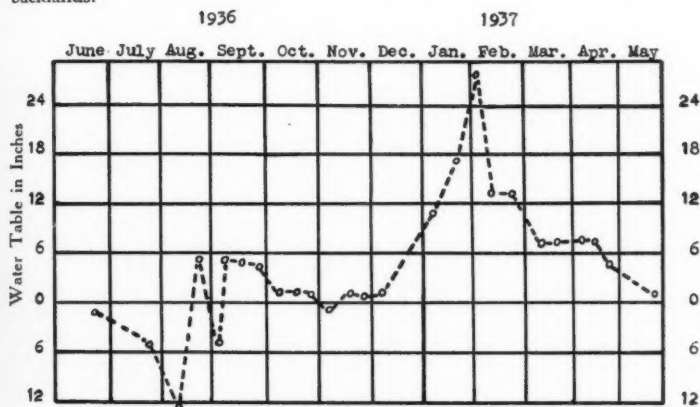


Fig. 5. Fluctuations in water level in the cypress-gum swamp.

WATER TABLE

The West Pearl River, at Indian Village, has an annual fluctuation in water level of approximately four feet, and, since the Indian Village Swamp is of the back water type (Viosca, '33), any change in water level in the river usually results in a corresponding change of water level in the swamp. During the period of this study (June, 1936-June, 1937), the West Pearl River reached its lower stages during the months of June, July and August, and it was during these months that the swamp, for the most part, was free of surface water (Fig. 5). The water table reached its lowest point in the first week of August when it was thirteen inches below the surface of the swamp floor. In the months of September, October, November and early December, the water in the swamp fluctuated from minus one inch to plus six inches, apparently due to heavy precipitation during this period of low river stages. At this time, the swamp partakes of the nature of a catch basin swamp serving as a reservoir for the immediate run-off from the pinelands. By the middle of December the West Pearl River began to rise, and near the end of January reached its peak for the season, at which time the water level in the swamp was recorded at twenty-eight inches. As the flooded valley was relieved of its

waters the water level in the West Pearl River gradually dropped during the latter part of February and continued to do so in March, April and May; during this period the surface water in the swamp also gradually receded and by early June of 1937 the swamp floor was again exposed.

WATER CONTENT OF SOILS

The water content of the back land soils was determined from samples which were collected near the end of the long hydro-period in order to indicate their water holding capacities. Weekly samples were collected during the month of April at depths of one, two, three and four feet from: (1) the older part of swamp about forty yards west of the levee of the West Pearl River, (2) the younger part of the swamp about fifty yards east of one of the marsh patches, and (3) from one of the marsh patches.

The per cent of water is based upon dry weight and was obtained by dividing the weight of the water in the soil by the actual weight of the dry soil. The value obtained is an expression of the number of units of water present for each unit of dry matter. The average per cent of water in the first foot of soil was less than in any of the lower samples, and the samples from the second foot level for each station exhibited the highest value. Below this latter level an increase in depth usually resulted in a decrease in the per cent of water of the samples. The average per cent of water in the first foot of soil was approximately the same in the older (197%) and younger (201%) parts of the swamp, but in the marsh patch it was much higher. The per cent of water in the second foot samples was more than twice that found in the first foot, the value for the older part of the swamp being 505 per cent and that of the younger part 542 per cent. The relationships are given in the following table in which each figure represents the average of four samples taken from the station and depth indicated.

Depth in Feet	Older Swamp	Younger Swamp	Marsh Patch
1	197%	201%	388%
2	505%	542%	542%
3	343%	346%	423%
4	289%	262%	496%

LOSS ON COMBUSTION

It has been shown that the per cent of water in saturated soils is closely related to the organic matter they contain (Penfound and Hathaway, '38). Therefore, it was deemed advisable to determine the per cent of material driven off during combustion which was present in the water laden backland soils. The same forty-eight samples which were utilized in determining the per cent of soil water present were used for the determination of organic content.

The average per cent of such matter present in the soils (based on four samples for each foot below the surface) was determined for the older swamp, the younger swamp, and the marsh patch. The samples from the first foot

of soil from each station contained less combustible material than any of the three lower samples of the same station. The smallest loss due to ignition (22%) was found in the first foot of soil in the older part of the swamp near the levee. In the younger portion of the swamp, farther west of the levee, the per cent of combustible matter increased to 27 per cent; and in the marsh patch still farther westward the very high figure of 42 per cent was reached. Thus in the older swamp, near the natural levee, where the greatest amount of alluvial deposition occurs, there is a relative, though not actual, decrease in organic matter accompanying the more rapid aggradation of this part of the swamp floor.

In both the older and the younger portions of the swamp at depths of both two and three feet the average loss on ignition is approximately twice that in the first foot at the corresponding stations. This great increase in combustible matter is apparently due to the presence of a pre-existing marsh which has been invaded by the swamp and subsequently buried by alluvium derived from the West Pearl River.

The results obtained in the study on loss of material due to ignition are given in the following table.

Depth in Feet	Older Swamp	Younger Swamp	Marsh Patch
1	22%	22%	42%
2	44%	51%	46%
3	39%	42%	51%
4	38%	36%	47%

SALINITY

The importance of the osmotic concentration of the soil solutions as the limiting factor in the distribution of some plant communities has long been recognized. In this study the total salinity of the soil solutions, of the surface water of the swamp, and of water from the West Pearl River was determined. The titration method was used in making the salinity determinations of the water samples collected.

Samples of the soil solutions of the back lands at Indian Village were collected in early August when the ground water table was near its lowest point (-11 in.) for the year, and hence, at this time the concentration of these solutions should be near the maximum for this area. Simultaneously, collections were made of water samples from the West Pearl River in order to compare its degree of salinity with that of the ground solutions. The average per cent of salt, based on eight separate samples, in the ground water of the back lands was 0.2 per cent, and the highest single value was 0.3 per cent. The West Pearl River at this time showed no measurable traces of sodium chloride and in subsequent analyses of its waters similar results were obtained.

Late in August when the back lands were covered with water (+7 in.) and, also, in April (+10 in.) samples of the surface water were collected. The results of these analyses indicate that the surface water is always free of any influential salt; and the highest value obtained in the surface water, cover-

ing the back lands, was 0.04 per cent. The above data indicate that the Indian Village swamp is influenced but very little by the saline waters of the Mississippi Sound. The community may therefore be termed a fresh water swamp since it lies in an ecologically fresh water area.

HYDROGEN ION CONCENTRATION

The pH values were determined for the surface water in the sawmp, the water of the West Pearl River, and the back land soils at depths of one, two, three, and four feet. In making these determinations a LaMotte-Morgan colorimetric soil-testing set was employed, and the surface and river waters were tested in the field, whereas the pH values of the soils from the back lands were determined in the laboratory.

The average pH values of the back lands at depths of one, two, three, and four feet are based upon six separate determinations for each foot. Samples were collected from the older swamp, the younger swamp, and the marsh patch, and because of the same general agreement of values, these were averaged in order to secure the average pH of the back lands at the various depths. The lowest average pH value was found in the first foot of soil (6.1) and with each succeeding foot this value gradually increased to a maximum of 6.7. An increase in the pH value indicates a decrease in acidity so that the above may be restated by saying that an increase in depth is accompanied by a decrease in acidity. The average pH value of the surface water of the swamp, based on eight samples, was found to be 6.5; and the average for the waters of the West Pearl River, based on five samples, was 6.9.

PHYTOSOCIOLOGICAL ANALYSIS

The structure of the cypress-gum community at Indian Village was studied by the list quadrat method of sampling. In making this study two sizes of quadrats were used, large quadrats (1 sq. chain) were employed for the woody vegetation, and small quadrats (1 sq. meter) were employed for the herbaceous species.

WOODY VEGETATION

The arborescent stratum of the Indian Village Swamp was studied by laying off ten consecutive quadrats, running from north to south, sixty-six feet on a side (1 sq. chain). These quadrats were situated approximately half way between the west levee of the West Pearl River and the marsh patches; the quadrats at the north end were in the older part of the swamp whereas those to the south were in the younger part of the swamp which lies in the vicinity of the fresh water marsh.

Each square chain was sub-divided into sixteen smaller quadrats, which were approximately sixteen feet on a side, in order to facilitate the counting and measuring of the trees, shrubs, and vines present. In making the counts two size classes were recognized; namely, (1) those individuals which were less than one inch in diameter at head height, and (2) those which had a diameter greater than one inch at head height. The diameter of the woody species was

taken at head height because this is just above the swollen bases of the trees and thus gives data which lends itself more favorably for comparison with other forest types. The diameter of a tree just above the swollen buttress is called the diameter at the bottleneck (D.B.N.) and this term is commonly used at the Southern Forest Experiment Station in New Orleans.

TABLE 1.—The number of individuals of the more abundant species per square chain. To express the number of individuals per acre multiply each figure by ten.

Species	Greater than 1 in. d.b.n.	Less than 1 in. d.b.n.	Total
<i>Nyssa biflora</i>	84	21	105
<i>Nyssa aquatica</i>	30	9	39
<i>Taxodium distichum</i>	24	9	33
<i>Rufacer drummondii</i>	6	6	12
<i>Fraxinus profunda</i>	0	7	7
<i>Cephalanthus occid.</i>	0	5	5
<i>Itea virginica</i>	0	5	5



Fig. 6. A view of the older part of the swamp near the West Pearl River.

The abundance or the average number of individuals of a species per square chain, distributed in two size classes, was determined from the data obtained for the ten quadrats studied. The results of this study show that black gum (*Nyssa biflora*) is the most abundant species present with a total of 105 individuals, tupelo gum (*Nyssa aquatica*) and bald cypress (*Taxodium distichum*) are the next most abundant species exhibiting respectively totals of 39 and 33 individuals per square chain. More abundant species and the distribution of the individuals into two size classes are given in Table 1. The arborecent species are not evenly distributed throughout the swamp. This is particularly true of the black gum. Individuals of this species, which often

grow in groups of three or four individuals, usually fuse from the ground to form stools and often the fusion occurs up to a height of six feet.

In conjunction with the density study the number of knees of bald cypress and of both species of gum were determined. The two species of gum knees were not differentiated in this study. The average number of *Taxodium* knees (Fig. 7) per square chain was found to be 73, and the average *Nyssa* spp. for the same area was 127. Thus, it is seen that *Nyssa* spp. knees are more abundant in the swamp. However, it must be recalled that the two species of gum constitute more than eighty per cent of the trees present and for this reason the average number of each type of knee per quadrat was divided by the average number of trees greater than one inch D.B.N. of each of the respective groups. This expresses the average number of knees present per tree. On this basis it was found that *Taxodium* has the greater number with 3 per tree, whereas *Nyssa* spp. averaged only 1 per tree.



Fig. 7. An interesting cypress knee from the cypress-gum swamp.

The diameter at head height (D.B.N.) of all the woody species present in every second quadrat was taken for all individuals which had a D.B.N. greater than one inch. The average D.B.N. was determined for each species and from these data the basal area of each species was calculated. Black gum possessed the largest average D.B.N. (5.52 in.) which was slightly greater than that of the bald cypress (5.1 in.).

The basal area was determined for each of the four species which had a D.B.N. greater than one inch, and is expressed in square feet per acre. In this study the basal area of a species is the sum of the cross-sectional areas, at head height, of all the individuals of that species found in one acre of the community. The basal area of the community was found to be 203 square feet and is approximately equal to that of a mature virgin long leaf pine associ-

ation which had a value of 205 square feet (Penfound and Watkins, '37). Black gum has a basal area (139.5 sq. ft.), approximately four times that exhibited by either of the other two abundant species. Black gum contributed 69 per cent of the total basal area, and the remaining 31 per cent was distributed through the other species as follows: bald cypress 16 per cent, tupelo gum 14 per cent, and red maple 1 per cent.

The average age of the cypress trees was 85 years but the age of the black gum trees was not determined. For a selected group of mature trees the average height of black gum was found to be 53.1 feet and the average D.B.N. for the same trees was 6.7 inches. Bald cypress averaged 50.7 feet in height, but possessed an average D.B.N. of only 5.4 inches (Table 2).

TABLE 2.—Tree height and the corresponding d.b.n. of the three species which contributed 99 per cent to the total basal area.

Species	Average Height	Average d.b.n.	Size Index
<i>Nyssa biflora</i> (18 trees)	53.1 ft.	6.7 in.	7.9
<i>Taxodium distichum</i> (20 trees)	50.7 ft.	5.4 in.	9.4
<i>Nyssa aquatica</i> (21 trees)	46.2 ft.	6.4 in.	7.2

The average height: diameter ratio (size-index) of each of the three dominants was determined by dividing the average height in feet of the trees, of each species, by the average D.B.N. of the same species. A comparison of the average size-indices indicates that bald cypress with a value of 9.4 grows more rapidly in height as compared with its diametric growth than does either black gum or tupelo gum with values of 7.9 and 8.2 respectively.

The frequency percentage as developed by Raunkiaer (Kenoyer, '27) is the value obtained by dividing the number of quadrats in which a species is encountered in a representative stand of the community by the total number of quadrats utilized. In this study the frequency values obtained are not indicative of the relative importance of the species encountered. Black gum, bald cypress, and tupelo gum constitute 99 per cent of the total basal area and yet have the same frequency value (100%) as pumpkin ash, which averages only six small individuals per quadrat, and exhibits an insignificant basal area. This seems to indicate that the size of the quadrats used for the study of the woody vegetation of the cypress-gum community is too large. Presumably a quadrat of one-fortieth of an acre in size would have been satisfactory. The decrease in size is desirable, as it will result in the displacement of the less abundant species from the highest frequency class to the lower frequency classes (Gleason, '29).

The woody species encountered in the quadrats were separated into two groups; (1) true swamp species, and (2) border species which occur in the swamp on elevated portions of the swamp floor, about the bases of trees, and upon *Nyssa* knees. The true swamp species include the first five species listed in Table 3, and also *Itea virginica* and *Cephalanthus occidentalis*. Most frequent species occurring on elevations in the swamp are vines which climb on the dominant swamp species (Table 3).

TABLE 3.—Frequency percentages for the species which occurred in the tenth-acre quadrats. Species marked with an asterisk are the border species which were noted in the swamp.

Species	Frequency percentage
<i>Nyssa biflora</i>	100
<i>Nyssa aquatica</i>	100
<i>Taxodium distichum</i>	100
<i>Rufacer drummondii</i>	100
<i>Fraxinus profunda</i>	100
* <i>Gelsemium sempervirens</i>	90
* <i>Toxicodendron radicans</i>	90
* <i>Cerothamnus ceriferus</i>	80
<i>Itea virginica</i>	80
* <i>Smilax walteri</i>	80
<i>Cephalanthus occidentalis</i>	60
* <i>Kraunhia macrostachys</i>	40
* <i>Styrax americana</i>	30
* <i>Ampelopsis arborea</i>	30
* <i>Smilax laurifolia</i>	20
<i>Fraxinus caroliniana</i>	20
* <i>Parthenocissus quinquefolia</i>	10
* <i>Cornus</i> sp.	10
* <i>Clethra alnifolia</i>	10
<i>Ilex decidua</i>	10
* <i>Rubus</i> sp.	10
* <i>Ilex opaca</i> (young, on <i>Nyssa</i> knee)	10

The species were grouped into five frequency percentage classes (1-20, 21-40, 41-60, 61-80, 81-100%) and the data conformed closely to Raunkiaer's Law of Frequency (Kenoyer, '27); $A > B > C < D < E$. The greatest number

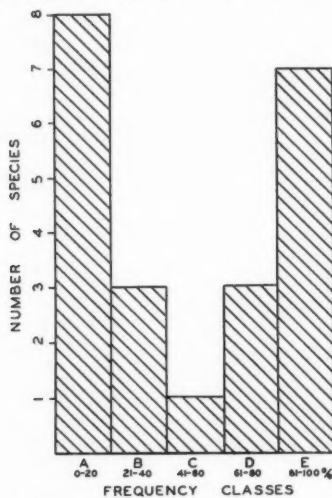


Fig. 8. Frequency diagram of woody species in the cypress-gum swamp.

of species (8) were found in class A ($8 > 3 > 1 < 3 < 7$). The relatively large number of species in class E can be attributed to the large size of the quadrats used. This is graphically illustrated in the frequency diagram (Fig. 8).

The species: area curve for the 1/10 acre quadrats was plotted and the minimal area was found to be somewhat less than one acre since ten such quadrats are more than sufficient to obtain practically all the species present in the community. However, due to the high degree of homogeneity of this community as indicated by the abundance, basal areas, and frequency diagram only one quadrat is necessary to obtain the important species present.

The crown cover was estimated at the beginning of the growing season and in the latter part of March in order to obtain some indication of the relative cover grade of the various species. The total crown cover just as the buds were opening was estimated at 20 per cent. Of this cover approximately 65 per cent is provided by the black gum, and the remaining 35 per cent is distributed throughout the other woody species present in the community. When the trees were in full leaf the cover was estimated at 60 per cent. The light intensity of the swamp was measured at the beginning of the growing season by means of a Leicameter and was compared with the light intensity over the West Pearl River during the same period. It was found that the light intensity in the swamp was only one-tenth as great as that outside. In early April when most of the leaves were present on the trees, the light intensity of the swamp was observed as being only one-twentieth of that in the open near West Pearl River.

The data obtained from the study of the woody species of the community indicate that this so-called cypress-gum swamp is in reality a *Nyssa biflora* consociates. *Nyssa biflora* is justly termed the dominant species of the community as a result of exhibiting: (1) the greatest number of trees per acre (55% of total), (2) the largest basal area (69% of the total), and (3) the greatest crown cover (65% of total). The two sub-dominants are bald cypress (*Taxodium distichum*) and tupelo gum (*Nyssa aquatica*).

TABLE 4—A comparison of the predominant trees in the cypress-gum community.

Species	<i>Nyssa biflora</i>	<i>Taxodium distichum</i>	<i>Nyssa aquatica</i>	<i>Rufacer drummondii</i>
Rank	Dominant	Sub-dom.	Sub-dom.	...
No. trees/acre greater than 1 inch d.b.h.	842	240	300	60
Basal area, sq. ft. per acre	139.5	32.7	29	1.8
Per cent. of total crown cover	65%	15%	8%	1%

HERBACEOUS VEGETATION

The herbaceous understory of the *Nyssa biflora* consociates was studied by the list quadrat method, each quadrat being one square meter. Fifty quadrats, at ten meter intervals, were established along a north to south line through the swamp approximately halfway between the natural levee and the marsh patches. Twenty-five of the quadrats were analyzed on March 21, 1937, and the

remaining quadrats were studied on April 11, 1937. The data, from these two sets of quadrats, were combined and treated as if fifty consecutive quadrats were studied in determining the cover and the frequency percentage of each species.

The frequency percentage of each species encountered in the small quadrats was determined by dividing the number in which the species occurred by the total number of quadrats investigated. The estimated cover of each species, when encountered in a quadrat, was recorded according to the following scale: x, present; 1, 1 to 5%; 2, 6 to 25%; 3, 26 to 50%; 4, 51 to 75%; and 5, 76 to 100%. The cover grade of each species in the community was determined by adding up the values assigned to each quadrat and dividing by the number of quadrats studied.

Mermaid-weed (*Proserpinaca palustris*) is the most frequent species (82%) of the understory and is the only species exhibiting an average cover grade as high as 2 (6-25%). The pretty spider lily (*Hymenocallis occidentalis*) which occurs in openings and appears to be very abundant, due to its conspicuousness, has a frequency percentage of only 22 and furnishes an insignificant amount of cover. In addition there were seven less frequent species which, collectively, contributed less cover than the two species above (Table 5). The infrequent or rare species which were not sampled in the quadrats included two submerged species: a bladderwort (*Utricularia inflata*) and the water-milfoil (*Myriophyllum heterophyllum*). Lizard's tail (*Saururus cernuus*) and pickerel-weed (*Pontederia cordata*) were conspicuous around the periphery of the swamp. The two smartweeds (*Persicaria portoricensis*) and (*Persicaria opelousana*), the waterleaf, (*Hygrophila lacustris*), and the white water lily (*Castalis odorata*) were noted in the swamp-marsh ecotone.

TABLE 5.—The frequency percentage and cover grade of the species which were encountered in the 1 square meter quadrats.

<i>Proserpinaca palustris</i>	81%	2
<i>Hymenocallis occidentalis</i>	22%	x
<i>Globifera umbrosa</i>	18%	x
<i>Utricularia macrorhiza</i>	10%	x
<i>Fraxinus profunda</i> (Seedlings)	6%	x
<i>Cephalanthus occidentalis</i> (young)	4%	x
<i>Hydrotrida caroliniana</i>	4%	x
<i>Justicia lanceolata</i>	4%	x
<i>Smilax walteri</i>	2%	x

Only nine species were encountered in the small quadrats and these were distributed through three of the five frequency classes recognized by Raunkiaer (Kenoyer, '27). Seven of these species fall in frequency class A (0-20%), and one each in classes B (21-40%) and E 81-100% (Fig. 9). The absence of species in classes C and D is not because the 1 square meter quadrats are too small for this study, but is due to the heterogeneity of the understory. The paucity of species of the understory probably can be attributed to a dense crown cover accompanied by a long hydroperiod which, together, are unfavorable to plant development.

The species: area curve for the understory begins to flatten off after the twentieth quadrat and no new species were added after the twenty-fifth quadrat was studied. This would seem to indicate that the minimal area for the herbaceous species is twenty-five square meters. However, it must be recalled that only one important species was found in the understory as indicated by the relatively high cover and frequency values. This leads to the belief that a representative picture of the floristic composition of this understory would be obtained within a minimal area of ten square meters if accompanied by a careful reconnaissance of the community for the infrequent species.

Epiphytes were abundant in the swamp. Bryophytic associations exhibiting vertical stratification are found growing mostly upon the lower forty feet of the tree trunks of the community. Along the edges of the swamp, and on slight elevations in the swamp, particularly on knees, and around the bases

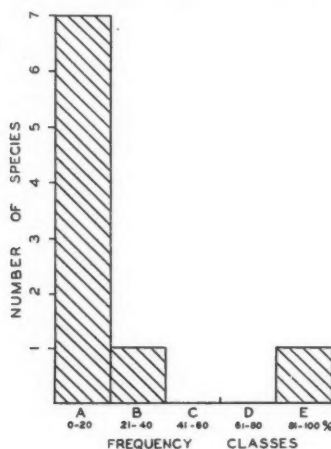


Fig. 9. Frequency diagram of herbaceous species in the cypress-gum swamp.

of trees, a community of *Pallavicinia lyellii*, either in pure stands or accompanied by *Odontoschisma* spp., is common. Decaying logs are rapidly clothed with *Riccardia pinguis* and *Riccardia latifrons* but these are rarely found on the knees or trunks of living trees.

In the swamp proper the most hydric community is that of *Fontinalis sullivanti* which inhabits the submerged portions of the bases of cypress and gum trees. Just above this microassociation is an exclusive community dominated by *Porella pinnata*. This continues to a point on the trunks where submergence is rare. From this level to a height of about thirty feet an open community comprising *Leucolejeunea clypeata*, *Leucolejeunea uniloba*, *Radula sullivanti* and other less frequent species is the rule. The upper portions of

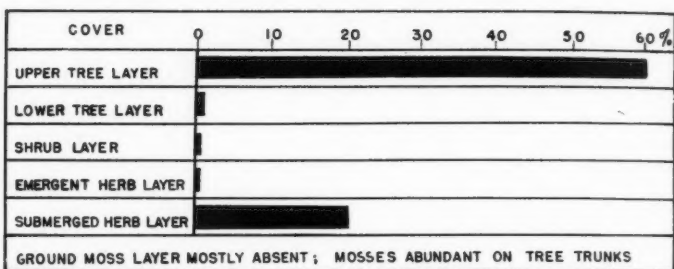


Fig. 10. Hult Sernander layering chart for the cypress-gum community investigated.

the trunks and some of the branches are populated with a fragmentary xeric community of *Frullania* spp.

Settlements of the tree fern (*Polypodium polypodioides*) are occasionally found on the trunks of the swamp trees, but they are not nearly as abundant or luxuriant as those found on *Quercus virginiana* near the periphery of the swamp. Another epiphyte noted as being present but not nearly as conspicuous as in the more mature cypress-gum community is the spanish moss (*Dendropogon usneoides*).

Summary

1. The community investigated is a fresh-water, marsh-successional cypress-gum swamp and technically is a *Nyssa biflora* consociates.
2. *Nyssa biflora* is the dominant species with bald cypress (*Taxodium distichum*) and tupelo gum (*Nyssa aquatica*) as subdominants.
3. The combined basal area of all trees greater than 1 inch d.b.h. is 203.0 square feet per acre.
4. A total of twenty-two trees, shrubs, and vines were found in the swamp, but only eight are recognized as true swamp species.
5. *Nyssa* and *Taxodium* knees are abundant in the shallower water of the swamp. The average number of knees per tree is three for *Taxodium distichum* and one for *Nyssa* spp.
6. Stools which are formed by the fusion of trees by the basal part of the trunks are commonly formed by *Nyssa biflora*, are occasionally exhibited by *Nyssa aquatica*, and are rarely developed by *Taxodium distichum*.
7. The intensity of light in the swamp at the beginning of the growing season is 1/10 of that on the outside. Later, when most of the leaves are present on the trees the light intensity in the swamp is only 1/20 of that outside.

8. The species of greatest abundance, frequency, and cover in the under-story is the mermaid-weed (*Proserpinaca palustris*).

9. The small number of floor species is due mainly to the great reduction in light intensity and the long hydroperiod.

10. Bryophytic associations exhibiting vertical stratification were noted on the lower forty feet of the tree trunks.

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Effect of Frequent Clipping on Plant Production in Prairie and Pasture*

J. E. Weaver and V. H. Hougén

The degeneration of native bluestem prairies of eastern Nebraska occurs slowly under moderate grazing or slight overgrazing but within two to five years where overgrazing is pronounced. Although the changes in the plant populations are continuous until the soil is finally almost bare, for convenience of study they have been grouped into several more or less distinct stages (Weaver and Harmon, 1935). An intermediate stage in deterioration is indicated by a great increase in the abundance of bluegrass (*Poa pratensis*), blue grama grass (*Bouteloua gracilis*), or buffalo grass (*Buchloe dactyloides*), the latter especially on low ground. Under long continued grazing and trampling, the native bluestems and most other prairie grasses disappear. This stage is characteristic of the bluegrass or short-grass pastures or a mixture of these. The purposes of this investigation were to ascertain the decrease in yield accompanying close grazing of virgin prairie, and to determine the relative yields of various types of prairie and of native pastures which replace them.

The clip quadrat method was employed, a total of 190 meter quadrats being used at six stations. Yield per unit area was determined at various intervals or at the end of the growing season. Height growth was used as a criterion of favorableness of environmental conditions, especially water content of soil and temperature, as well as an indicator of the effects of overgrazing. Dry weight of plants is one of the best quantitative characteristics of vegetation (Hanson, 1938), and increase in dry weight is the best measure of growth (West, Briggs, and Kidd, 1920). The clip quadrat has been widely used by numerous American investigators (Sarvis, 1923; Taylor and Loftfield, 1924; Aldous, 1930; Black, *et al.*, 1937) and has been found to be the most suitable form of the percentage production method on the grassveld in South Africa (West, 1936).

Although clipping studies serve as a valuable supplement to grazing experiments, they differ in several respects from actual grazing. The chief differences as observed by Culley, Campbell, and Canfield (1933) and others have been summarized by Weaver and Clements (1938) and the fact pointed out that clip quadrats are widely used.

In the early spring of 1933, typical experimental plots were selected in the several types of prairie and pasture at Lincoln, Nebraska. Enclosures were established and groups of meter quadrats laid out before the grasses resumed growth. The position in which the quadrats were placed was given careful consideration. The areas selected after years of acquaintance with the vegeta-

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tion were thoroughly representative of the conditions it was desired to study. The quadrats were located on typical sites to represent average conditions. The vegetation was clipped close to the ground with a pair of shears, care being taken not to injure the crowns. Although this treatment seemed severe, it was similar to grazing by cattle and horses confined to a portion of the same prairie which was fenced for pasturing in 1933. Similar close grazing was common nearly everywhere in the drought-stricken pastures and prairies of Nebraska and Kansas during 1934 to 1937.

LOCATION OF PLOTS

Little bluestem (*Andropogon scoparius*) consociation and the big bluestem (*A. furcatus*) consocieties were the two most extensive types of grassland occurring in true prairie. Because of their importance, three stations were selected in these types. One was in a nearly pure stand of little bluestem on a gentle north facing slope in the Belmont prairie just north of Lincoln. Small amounts of *Andropogon furcatus*, *Sorghastrum nutans*, *Poa pratensis*, and a few other grasses were present but forbs were not abundant. A second station was established on the lowland about a mile distant in an area of nearly pure *Andropogon furcatus* with small amounts of *Sorghastrum nutans*. A third occupied a west-facing slope in the Belmont prairie where the more mesic big-bluestem type at the foot of the hill first merged with and then gave way to the little bluestem and accompanying mid grasses on the upper slope. Three other stations were also selected: one in an adjoining upland pasture where *Bouteloua gracilis* and *Buchloe dactyloides* had replaced the bluestems, a second on the pastured lowland where these short grasses also occurred in nearly pure stands, and the third in a lowland pasture where the prairie grass had been replaced by bluegrass. All six stations were within an area of one square mile, hence aerial conditions were fairly similar. The upland soil is Lancaster loam, a mature soil of rolling topography derived from the Dakota sandstone formation. That of the lowlands is a colluvial phase of Wabash silt loam, immature, but deep and fertile. At the big-bluestem station it contained considerable sand.

WATER RELATIONS

Growth in the true prairie is so closely correlated with soil moisture, that a knowledge of the water relations is necessary to an interpretation of plant production. The year 1933 was preceded by one very favorable to growth, only one or two weekly periods during summer being without rainfall. With a single exception in the surface six inches, water was continuously available, at least in the amount of 3 to 5 per cent, at all depths to which the roots of grasses penetrate. Thus, the vegetation was in a vigorous condition when the experiment began.

Spring and early summer of 1933 were rather dry but there was much rain in July, drought during August, and an abundance of moisture late in August and in September. Available water content in the surface foot was nearly exhausted in June, but the deeper soil was continuously moist. Following an

abundance of moisture during midsummer, the surface soil became drier and dry soil extended deeper during the middle of August. This period was followed by abundant rainfall.

Water content of soil showed a deficiency during 1934. Following a dry winter, the rainfall in March was light. The heaviest rain in April or May did not exceed .24 inch. The entire summer was extremely dry, precipitation of only 2.47, .40, and 2.59 inches being recorded for June, July, and August, respectively. The abundant water supply in the first two feet of soil was greatly reduced during May and entirely depleted by midsummer. The moderate to small reserves of the deeper soil in spring were likewise greatly reduced in June and entirely depleted to a depth of 4 feet in August, the deeper soil to 6 feet retaining less than 2 per cent available moisture. Below 6 feet depth, moisture was constantly available throughout the drought, but only in small amounts. Drought continued during the winter and was not ameliorated until the following April.

The early spring of 1935 was dry, but rainfall of May, June, and July averaged about normal. Drought occurred during August. A fair to good water content of soil in spring and early summer promoted excellent growth. Soil moisture was depleted in August and the vegetation dried and practically ceased to grow.

STATION IN LITTLE BLUESTEM

A series of 20 quadrats was staked out in two groups of 10 each. The quadrats were spaced in such a manner that a distance of 12 inches intervened between the individuals in each row. They were in four parallel rows only a few feet distant. Five in each group were clipped, together with a marginal area 12 inches wide around each quadrat to insure lack of competition, and 5 only at the end of the growing season. This portion of the prairie had not been mowed the previous summer, but was burned early in the spring.

After each clipping, the plants renewed growth within a few days, the rate of growth varying chiefly with the water content of the soil. At the first cutting, on May 9, for example, the grasses were only 1.5 to 3 inches tall; at the second (May 27) about 5 inches, but on June 25 they averaged 7 inches in height. Even greater height (8 to 10 inches) was attained in July, but growth was progressively less thereafter. Growth of little bluestem in undisturbed, adjacent areas during the summer was determined at 7- to 15-day intervals by Flory (1936). Little bluestem increased from 1 inch in the single-leaf stage on April 26 to 11.5 inches on June 8. A height of 24 inches was attained by August, and about 40 inches when the flower stalks were fully developed in September.

Yields from the several quadrats were quite uniform, although not so high as during years of greater rainfall. The yield of the 10 control quadrats, cut on October 10 before the first killing frost, averaged 348 grams. This was 37 grams or 10 per cent less than the average yield from the quadrats clipped six

times. The increased yield from the clipped quadrats (Table 1) resulted in depletion of food reserves (Bukey and Weaver, 1938).

TABLE 1.—Yield in grams of air-dried material of clip quadrats of little bluestem during 1933.

No.	May 9	May 27	June 25	July 27	Aug. 27	Oct. 10	Total
1	20.4	61.0	111.0	118.8	75.7	22.0	408.9
2	21.4	54.5	91.8	115.0	71.2	24.8	378.7
3	17.0	66.0	89.8	112.1	78.0	27.4	390.3
4	12.8	59.0	76.2	100.6	69.7	24.2	342.5
5	20.0	76.5	114.0	118.2	76.8	22.4	427.9
6	19.6	77.5	109.8	115.7	73.7	21.1	417.4
7	21.0	73.0	99.2	120.9	79.4	23.1	416.6
8	18.2	67.7	88.5	108.8	62.0	22.2	367.4
9	17.0	66.2	70.0	109.1	60.9	19.1	342.3
10	19.5	61.7	78.8	114.0	66.4	20.3	360.7
Ave.	18.7	66.3	92.9	113.3	71.4	22.7	385.3
% yield 5	17	17	24	29	19	6	100

The late date of renewed activity of little bluestem is shown by its growth which was only 5 per cent of the season's yield on May 9, and 22 per cent by the end of May. The greatest growth occurred during June and July (53 per cent), it continued rather high during flower-stalk production in August, but was only 6 per cent thereafter. Flory (1936) has shown that the mean monthly production of dry matter (1931 to 1933 inclusive) of undisturbed prairie vegetation at this station was 2 per cent in April, 26 in May, 36 in June, 21 in July, 13 in August, but only 2 per cent in September.

During 1934, the clip quadrats of the preceding year were again clipped, but only 4 times, because of the extreme drought. The quadrats that were clipped but once, at the end of 1933, were also clipped 4 times, while a new lot of 10 adjacent quadrats was used as a control and cut only at the end of the season. The old growth of the previous year had been removed from them in early spring. Thus, in the fall total yields were had (a) from quadrats closely clipped for two seasons, (b) from those closely clipped one season, and (c) from unclipped controls.

Late in April, little bluestem in quadrats closely cut the preceding year was only one-half as tall as that in the controls, where it averaged 2.5 inches. Other plants gave similar differences. Moreover, the basal cover was sparser (Figs. 1 and 2). The low yields at the first clipping, on May 14, were the result of a poor early growth. Grass in the control quadrats was 5 to 8 inches tall, but that in the closely clipped ones only 2 to 5 inches. The clipped bunches were not filled with stems as were the controls, frequently they had living stems only around their borders.

Further study on June 2, after a single clipping, gave the following differences in height of grasses in the control, those clipped once in 1933, and those clipped closely in 1933 and 1934: little bluestem, 4 to 9, 2.5 to 5, and 2 to 4 inches, respectively, and big bluestem 8 to 11, 5 to 9, and 3 to 5 inches, in

the same sequence. With more frequent clipping, thinness of basal cover and an increasingly yellow-green color of the vegetation were clearly evident.

At the second clipping, on June 13, little bluestem was only 3 inches tall in quadrats clipped regularly the previous year, 5 to 8 inches in those clipped but once, but 6 to 10 inches in the new controls.

Grasses in the control quadrats were dried and had taken on their autumnal colors by July 22.* Those in quadrats clipped for the first year were 3 to 6 inches tall and, although somewhat wilted, they were fairly green. In quadrats cut closely the preceding year, plants were only 2 to 4 inches tall and the thin foliage was fresh and green. Clipping had reduced the water loss by transpiration and soil moisture was still available. Only 15 per cent of the total crop was produced after the third cutting on July 22.

The ten quadrats clipped only on October 20, gave an average yield of 135.5 grams. This was only 39 per cent as much forage as the ten control quadrats yielded the previous year. Except for a slight development following rains of September first, very little growth occurred after June 13, 1934. These new control quadrats yielded 20 per cent less than those clipped frequently for the first time in 1934, which produced an average of 170.2 grams. The grasses in the unclipped quadrats exhausted the available supply of water within reach of their roots earlier than did those whose demands for transpiration were frequently reduced by clipping. Hence, their growth continued slowly after the unclipped grasses had dried. Quadrats clipped frequently for a second year yielded only 68.7 grams or 51 per cent as much as the controls. Although these grasses also remained green, even after those clipped for the first year had finally dried, accumulated food was too greatly depleted to permit of much growth.

Cutting in 1935 was delayed until June 15. This was because of the severe drought of the previous summer which continued well into the spring of 1935. After two years of continuous close clipping, little grass remained alive. Clipping experiments on blocks of prairie sod (Biswell and Weaver, 1933) have clearly shown that few new roots are produced, while studies by Peralta (1935) on Sudan grass show that repeated clipping results in the death of the deeper root system somewhat in proportion to the number of cuttings. Little bluestem in the quadrats had nearly all died (Figs. 3 and 4). *Poa pratensis* showed an increase, big bluestem withstood the drought and close clipping quite well, and considerable side-oats grama (*Bouteloua curtipendula*) had appeared. The general grass level in the closely cut areas on June 15 was 4 to 8 inches. A thicker stand of grasses remained in quadrats cut closely but one year and the height was 7 to 10 inches. The stand was much denser in the control areas where the grass was 12 to 15 inches tall.

Abundant soil moisture resulted in good growth until terminated by drought about July 10. The quadrats were clipped six days later. The plants

* A complete description of the response of the prairie to the great drought of 1934 is given by Weaver, Stoddart, and Noll, 1935.

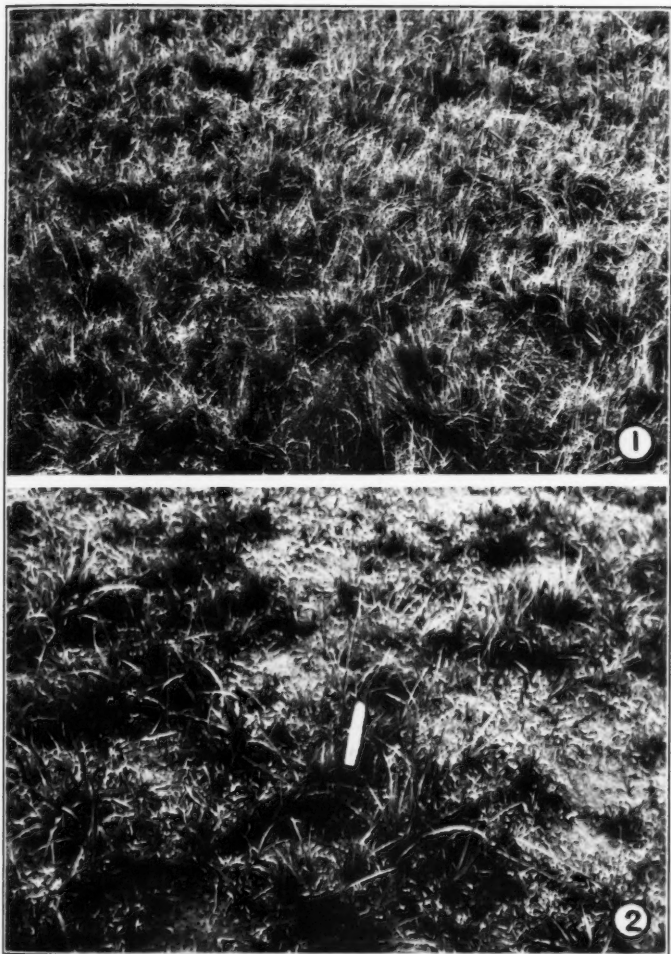


Fig. 1. Prairie at the little-bluestem station after mowing in the fall of 1933. Fig. 2. Similar area on Sept. 15, after one year of close clipping.

were so weakened and drought so severe that at the time of the last cutting, on September 10, the respective heights of foliage in areas cut two and one years and the controls were only 4.5, 5 to 7, and 16 to 20 inches. Flower stalks of little and big bluestem in the control quadrats were 30 and 40 inches tall, respectively. Yields are shown in Table 2.

TABLE 2.—Average yield in grams of air-dried material of quadrats of little bluestem during 1935.

Quadrats	June 15	July 16	Sept. 10	Total
Closely clipped 1933 and 1934	86.1	51.6	48.3	186.0
Closely clipped 1934	196.4	70.0	53.4	319.8
Controls			588.8	588.8

Examination of Table 2 shows not only the greatly decreased yield at each cutting of the quadrats most frequently clipped, but also the great decrease in total yield. Quadrats clipped during two preceding years produced only 58 per cent as much as those clipped during a single preceding growing season. Compared with the controls, the yield was only 32 per cent as great. Yield of plants clipped for two years was 54 per cent of that of the controls. Moreover, change in population was marked. Both bluestems practically disappeared and were replaced in part by side-oats grama. During 1936 this species formed a nearly pure, open stand, and indicated clearly its great increase which occurred over wide areas following the great drought.

Résumé

The year 1933 was only intermediately favorable to growth (yield of controls, 348 grams); 1934 was poorest (135.5 grams), and 1935 best (588.8 grams). The remarkable manner in which the grasses renewed growth after each of six cuttings the first year should be emphasized. Moreover, the yield of the several cuttings totaled 11 per cent greater than that of the controls. That this growth was made at the expense of reserve foods was clearly revealed by the reduced vigor and yield as well as by the high death rate the following season.

New controls the following year were again outyielded by new quadrats clipped four times. But yields from the grasses exhausted by frequent clipping during the preceding year were only 51 per cent as great as that of the controls, and 60 per cent less than quadrats clipped frequently for the first time. During the third year, quadrats clipped for a second year yielded only 54 per cent as much as the controls, and those clipped for a third year only 32 per cent as much. The effects of continuous close clipping are again shown by the fact that the quadrats clipped for a third year yielded only 58 per cent as much as those clipped two years. That two-thirds of the possible forage yield may be lost and the plants so greatly weakened by overgrazing for only three years is alarming. Yet the phenomenon, often intensified, has occurred in thousands of prairies and pastures throughout the west where drought left the ranges greatly overstocked.

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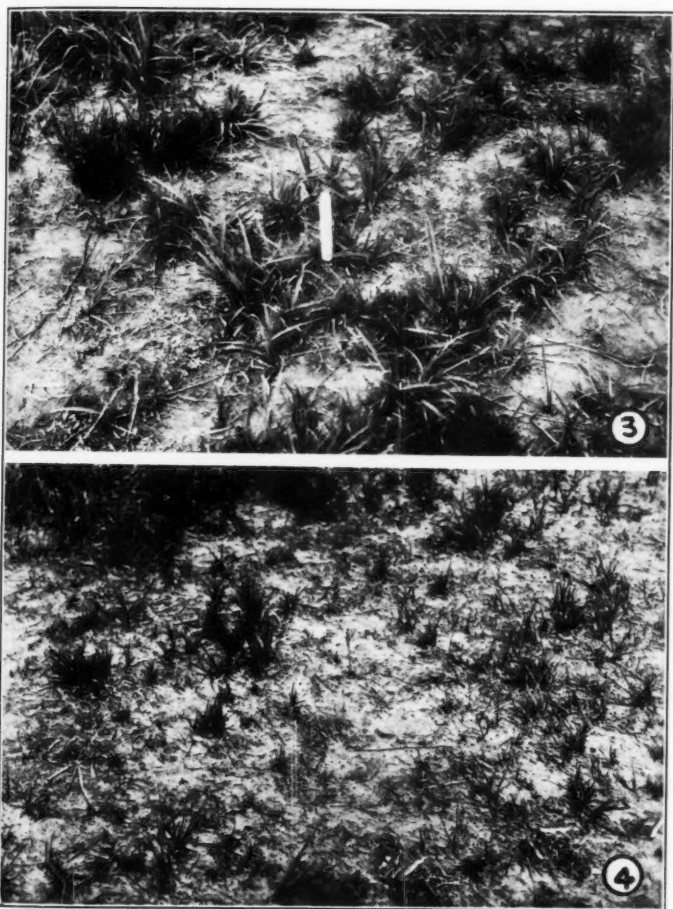


Fig. 3. Little bluestem quadrat on Sept. 10, after two years of frequent clipping.
Fig. 4. Similar quadrat after the vegetation had been clipped at frequent intervals for three seasons. Comparison with Fig. 1 reveals the almost complete destruction of the vegetation.

STATION IN BIG BLUESTEM

A group of 20 meter quadrats was selected for average cover on a plot of low, nearly level land on the flood plain of Salt Creek. The prairie had been mowed annually in September for a long period of years.

At the first cutting (May 9) the grass was only 1 to 4 inches high; at the second, on May 27, it was 4 to 7 inches tall, and at the third clipping, June 25, the foliage had again reached a height of 4 inches. In the control quadrats the grasses had attained a general level of 18 inches and a maximum height of 2 feet. This was about the normal height growth compared with that of previous years. At the fourth cutting (July 27) the average height was 6 inches, although a few flower stalks were 12 inches tall. On August 27, the grass had again reached a height of 7 inches; a few flower stalks were 18 inches tall and in the "boot" stage. *Euphorbia maculata* had become a bad weed forming 5 to 60 per cent of the basal cover. The general level of the controls was 32 inches but the flower stalks were about 5 feet tall.

The average yield from 10 control quadrats, cut on October 20, was 668.3 grams. This exceeded the average of the total partial yields (407.8 grams) by 64 per cent, differences being emphasized by the weight of the numerous flower stalks of the controls. Percentage distribution of yield was somewhat similar to that of little bluestem for the same season, being 9 per cent less during June and July and 5 per cent greater in August.

During 1934, three groups of 10 quadrats each were used. Those cut repeatedly in 1933 were clipped 4 times in 1934; the controls of 1933 were similarly clipped; and a new group of 10 quadrats was used as a control.

At the first cutting (May 15) the grasses in the control quadrats of the previous year were 6 to 10 inches high, those in the closely clipped ones only 3 to 5 inches. The latter were doing poorly and showed a greater invasion of bluegrass. By the first of June, the general level of big bluestem in the clip quadrats was 5 inches, that in the controls was 11. Although the drought was severe and growth retarded, the relatively shallowly rooted bluegrass was the only species that showed distress. At the time of the third clipping (July 22) the vegetation in the quadrats closely clipped in 1933 was very thin; the average height was about 5 inches. Lack of uniformity in growth was due in part to the drought since this was clearly apparent in the control quadrats as well, where the big bluestem was 8 inches tall and beginning to dry. In September, the grass in the control quadrats was only 10 to 12 inches tall. The areas closely clipped in 1933 had a new growth of 2 to 6 inches; but the grass in those cut frequently only during 1934 was 4 to 8 inches tall and the stand was much thicker.

The control quadrats on October 20 gave an average yield of 139.7 grams, which was only 21 per cent of the yield of the controls of the preceding year. Thus, the relative yield was reduced even more greatly than on the upland where the dry weight was 39 per cent as great as that of the 1933 controls (Table 3).

TABLE 3.—Yield in grams of air-dried material of clip quadrats of big bluestem during 1934.

Quadrats	May 15	June 13	July 22	Sept. 27	Total
Clipped 6 times, 1933	32.8	27.9	16.5	23.0	100.2
Per cent yield	33	28	16	23	100
Clipped once, 1933	56.4	42.1	32.0	27.6	158.1
Per cent yield	36	27	20	17	100
Controls	---	---	---	---	139.7

Quadrats clipped in 1934 yielded 158.1 grams, which was 13 per cent more than the controls. This was due to an expenditure of reserve foods in repeated renewal of growth, and to an increased soil-water reserve resulting from a decreased transpiring surface. Quadrats clipped for a second year gave an average yield of 100.2 grams which was only 72 per cent as great as the controls, and but 63 per cent as much as quadrats clipped closely only a single summer. Thus the destructive effects of continued clipping were clearly apparent. Owing to the burial of the area during the late summer of 1935 during artificial deepening of the creek bed, further data were not obtained.

Résumé

Behavior of big bluestem under frequent clipping resulted in continually renewed growth. Since the coarse, heavy flower stalks were not formed because of six clippings, these quadrats yielded only 61 per cent as much forage as the controls. But during the drought year (1934), when even the controls produced few flower stalks, the yield of four clippings from a new lot of quadrats exceeded that of the controls by 13 per cent. Thinning of the grass after a single year of clipping was marked and infestation of weeds pronounced. The yield during a second year of cutting was only 72 per cent of that of undisturbed quadrats. Quadrats clipped a second year yielded only 63 per cent as much as those similarly treated for a single year.

HILLSIDE STATION IN LITTLE AND BIG BLUESTEM

A portion of the Belmont prairie on rather hilly land had been fenced and used as pasture for cattle and horses. It was closely grazed for a single year (1932), after which a large enclosure was fenced against livestock. A similar, adjacent, ungrazed area in the prairie was also set aside for experimental purposes. These contiguous enclosures occupied a rather steep (10°) west-facing slope. Twenty representative meter quadrats were selected in the prairie and a similar number in the pasture. In both plots they extended from the top to the bottom of the slope. Alternate quadrats were clipped six times during 1933 and the remainder (controls) once, at the end of the season.

Renewal and rate of growth after clipping were similar to that at the preceding stations. Big bluestem grew about twice as rapidly as little bluestem which was also the first to degenerate and disappear. The quadrats, as

would be expected, gave an increase in yield from the top to the bottom of the slope. The average total yield of those cut six times was 332.9 grams. This was 2 per cent less than that of the controls (340 grams). In neither lot was the average yield as great as that from the quadrats on the gentle north hillside of the same prairie. The percentage seasonal yield was similar to that of the bluestems already recorded.

From observations in the pasture, it was evident by the middle of June that the bluestems had been handicapped by a single year of heavy grazing and trampling. Only remnants appeared above ground. Often the bunches and sods were merely outlined by living stems. Bluegrass, benefiting by the decreased competition of the native species, had increased rapidly. It partially filled the interspaces between the old prairie grasses, and, especially on the lower slopes, often formed a dense sod. By the end of the year it was in major possession of the entire lower slope. The dry season, however, was distinctly disadvantageous, the bluegrass appearing dead late in June.

The average total yield of the closely clipped pasture quadrats was 246.8 grams; yield of those clipped at the end of the season averaged 248.0 grams. This was a difference of less than 1 per cent from the yield of those clipped 6 times. Yields from these control pasture quadrats cut in October showed a decrease of 27 per cent over those similarly treated in the prairie. This decreased yield may be attributed directly to close pasturing in 1932. Percentage seasonal distribution of yield was similar in prairie and pasture.

Late in April of 1934, the prairie on the hillside was burned slowly against the wind. None of the cut quadrats in either prairie or pasture had enough materials to support a fire, but in this way a third lot of quadrats was cleared for use as a control in the prairie during 1934.

By May 13, one could easily select the clip quadrats of the preceding year in the prairie. Grasses and forbs were both greatly dwarfed. The stand was very open, and the grasses were only 2 to 5 inches tall as compared with 5 to 8 inches in quadrats cut only in the fall, where there was also a greater basal cover. In the clip quadrats *Poa pratensis* showed a marked increase on the lower slope and *Bouteloua gracilis* on the upper one. By midsummer all of the bluegrass and little bluestem had died on the mid and upper slope, but much of the more deeply rooted big bluestem survived.

The average yield of the ten new control quadrats, clipped on October 10, was 143.1 grams. This yield was only 42 per cent as great as from the ten control quadrats during the preceding year. Average yield from the previous controls, closely cut 4 times this season, was 139.5 grams, which was about 2 per cent less than the controls. The very low average yield (68.1 grams) from quadrats clipped two years was only 49 per cent of that from quadrats clipped during one year, and 48 per cent of the yield of the controls.

The pasture quadrats grazed or closely clipped for three consecutive years yielded only 39.5 grams. Those closely grazed one year, protected one year, and frequently clipped in 1934 yielded 97.5 grams or approximately 2.5 times

as much. The pasture yields, compared with those in prairie were, respectively, only 58 and 70 per cent as great.

The pasture had deteriorated so greatly that further studies were not made. In the prairie, data were secured during 1935 as shown in Table 4.

TABLE 4.—Yield in grams of air-dried material of clip quadrats from the bluestem hillside-prairie during 1935.

Quadrats	June 15	July 16	Sept. 11	Total
Clipped closely in 1933 and 1934	117.6	58.0	13.9	189.5
Clipped closely in 1934	150.1	68.5	25.9	244.5
Clipped once in 1934	426.6

Casual examination of Table 4 shows clearly the marked effects of continual clipping. Decreases from the control of quadrats closely clipped during two years were 43 per cent, and for three years (1933 to 1935 inclusive) they were 56 per cent.

Résumé

The yields from the mixed stand of little and big bluestem on the more xeric west slope were not greatly different from those afforded by little bluestem on the north hillside, except during the third year when they were about one-fourth less. During the first year, yields from both prairie and pasture were similar in that the dry-weight production from clipped and control mixed bluestem quadrats was only one or two per cent different. Yield from the year-old pasture, however, was approximately only 74 per cent as great. Here also invasion of bluegrass following the weakening of the bluestems was marked.

Yields of prairie quadrats clipped one and two years, respectively, were 98 and 48 per cent of the controls. Thus, a second year of clipping reduced the yields over those of one year by one-half. Quadrats in the pasture (protected one year after a single year of grazing) when frequently clipped yielded only 70 per cent as much as those in prairie. Quadrats grazed in 1932 and clipped in 1933 produced in 1934 only 58 per cent as much as prairie quadrats clipped two years. This illustrates the cumulative evil effects of too frequent utilization of the forage.

Quadrats in prairie clipped during two and three years, respectively, yielded in 1935, 57 and 44 per cent as much as the controls. Those clipped for three seasons produced only 77 per cent as much forage as those with two years of such treatment.

UPLAND STATION IN SHORT-GRASS PASTURE

A series of 40 quadrats was established in a pasture adjoining the Belmont prairie, which about 15 years earlier formed a portion of this unbroken tract. Because of the continued impact of grazing, considerable areas on the hill-sides had degenerated into an almost pure stand of short grasses, mostly *Bouteloua gracilis* but some *Buchloe dactyloides*. Two separate plots about

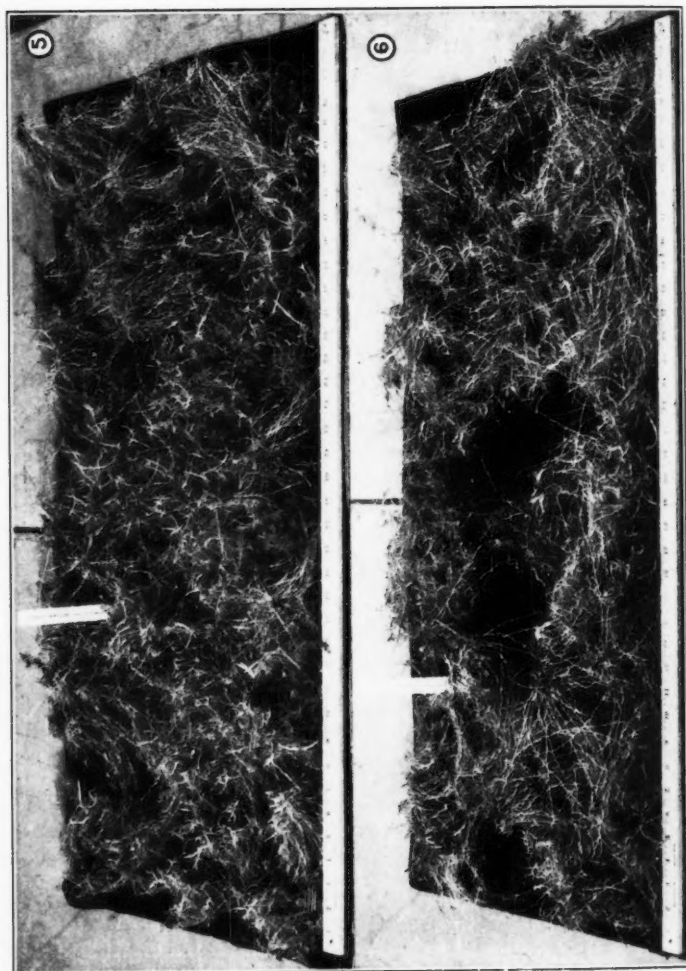


Fig. 5. Underground parts of big bluestem from one-half of a control quadrat on level lowland. Fig. 6. Materials from one-half of a quadrat closely clipped for two years.

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one-fourth mile distant, each 0.5 acre in extent, were fenced and 20 representative quadrats were selected in each plot. Alternate quadrats were clipped five times during the growing season and the remainder once, in October.

The grasses were 2 inches tall at the initial cutting on May 10, 1933, and 2 to 4 inches on June 3. Late in June there was too little regeneration to warrant clipping, but the previously clipped grasses were green although those in the control quadrats were half dried. By July 15, a height of 1 to 1.5 inches had been attained, and, after clipping, the new growth was 2 inches tall late in August. Some flower stalks 4 to 12 inches tall had been developed by the blue grama grass. Only a little growth was made after the fourth cutting on August 27. Final harvest was on October 12.

The quadrats gave considerable differences in yield probably due to irregularities in previous grazing, local soil conditions, etc. The average yield from the one cutting of 20 quadrats was 181.7 grams; the average total of the partial yields from the 20 clip quadrats was 192.4 grams, or 6 per cent greater.

LOWLAND STATION IN SHORT-GRASS PASTURE

A portion of the pasture adjoining the prairie extended over level, rather low ground. It had formerly been occupied by *Andropogon furcatus*, *Sorghastrum nutans*, and smaller amounts of *Panicum virgatum*. A part of this pasture presented a disclimax of nearly pure stands of blue grama grass and buffalo grass. The accumulated debris on these areas was burned with a slow fire on a damp day. Twenty quadrats were then staked out in selected typical areas.

On May 10, the short grasses were only 1 to 2 inches tall. In general, height growth was greater than that on upland. At the October cutting, the height of foliage ranged from 2 to 3.5 inches, and flower stalks of blue grama were about 17 inches tall. Weeds were sparse or absent.

About the same proportion of grama grass and buffalo grass occurred in both clip quadrats and controls. The yields of both grasses varied widely, depending largely upon the basal cover, which ranged from 52 to 80 per cent. The quadrats cut five times gave an average total yield of 276.6 grams; those cut but once 212.2 grams. Thus, the yield of the former was 30 per cent greater.

LOWLAND STATION IN BLUEGRASS PASTURE

Other portions of the lowland area were clothed with a pure stand of bluegrass. It was lightly grazed in 1932 but fenced and burned in early spring of 1933. Ten quadrats were staked for close cutting and ten alternate ones to be cut only at the end of the growing season. Cuttings were made on May 1, June 4, July 14, August 27, and October 9; the partial percentages of the total yield at each cutting were 16, 16, 9, 46, and 13, respectively. The marked differences in yield of the several quadrats (203 to 393 grams) are characteristic of old bluegrass pastures. They often result from irregularities in grazing because of dung and the stimulating effect the latter has upon the yield.

The total average yield from the five cuttings was 274.8 grams or 5 per

Fig. 5. Underground parts of big bluestem from one-half of a quadrat closely clipped for two years.

Fig. 6. Materials

cent more than that from the one cutting (263.0 grams) of the control quadrats.

Growth of bluegrass in early spring of 1934 was good but extremely dry weather ensued and the grass not only ceased growing but died.

Résumé

Dry weight production in both the upland and lowland short-grass areas as well as in the bluegrass pasture was greater (6, 30, and 5 per cent, respectively) from quadrats clipped five times than from the single seasonal cutting. Compared with production of the clip quadrats of the little bluestem during the same season, the respective yield in the upland pasture was only 50 per cent as great. Yields from the short-grass and bluegrass, lowland pasture were only 68 and 67 per cent as great, respectively, as were those from the big-bluestem lowland prairie similarly clipped. These data indicate great losses in forage when bluestem prairies are permitted through misuse to degenerate either into short-grass or bluegrass pasture.

EFFECTS OF FREQUENT CLIPPING UPON WEIGHT OF UNDERGROUND PLANT PARTS

Samples of sod, each one-half square meter in area and 10 centimeters deep, were secured from certain control quadrats and from others clipped during one or more years. The soil was carefully washed away and the stem bases, roots, and rhizomes entirely freed from adhering soil particles (*cf.* Weaver and Harmon, 1935). Control quadrats of little bluestem gave an average yield of 435 grams per sample of air dry underground plant parts. Decrease in dry weight of this plant material, based on the control, was 41 per cent after two seasons of close clipping and 59 per cent by July 25 of the third year. Moreover, much of this material was dead in 1935.

Similar samples of big bluestem are shown in Figs. 5 to 7. The sample from the control quadrat had a dry weight of 445 grams. Dry weight from the quadrat closely clipped two years was 33 per cent less and reduction in weight increased to 57 per cent by the middle of the following summer. Since the second sample and especially the third contained much dead material which was very light when dried, the losses in weight are even greater than indicated in the Figures.

DISCUSSION

Grazing, or clipping to simulate grazing, is a more or less destructive process since it removes much of the photosynthetic area from the plant. Preservation of pasture grasses depends upon manufacture and storage of foods by the plants in excess of those consumed in growth. Whenever grazing is so intensive that it permits complete and frequent removal of the green shoots it greatly reduces the manufacture of carbohydrates and prevents their storage in underground parts. Such abrupt decrease in photosynthetic activity causes a corresponding decrease in the growth of roots. Continued defoliation is extremely injurious and unless reasonable precautions are taken to

prevent it the effects are likely to become cumulative and cause serious deterioration of pasture or range. This may be followed by erosion, loss of nutrients, and general impoverishment of the soil.

Results from studies on the effects of the removal of the photosynthetic area are in agreement that the yield and vigor of the vegetation vary inversely with the frequency of clipping. Aldous (1930) applied clipping treatments at two-week intervals to prairie grasses (chiefly big and little bluestems) at Manhattan, Kansas. He found that the density of the vegetation decreased about 60 per cent in three seasons. Clipping at three-week intervals resulted in only 13 per cent reduction. Disappearance of valuable species was proportional to frequency of cutting. The higher nutritive value of the forage gained from frequent harvesting did not compensate the loss in yield.

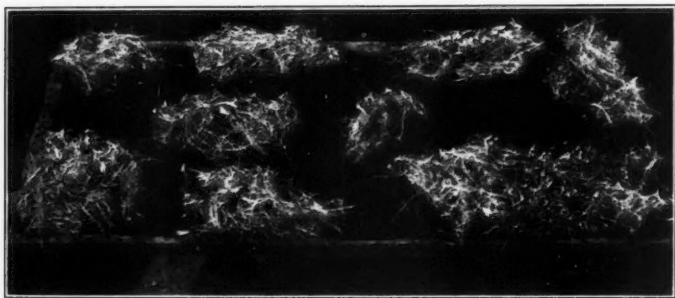


Fig 7. Roots and rhizomes from one-half square meter of big bluestem closely clipped for 2.5 years. The dry weight decreased from 445 grams (Fig. 5) to 296 grams (Fig. 6) and, finally, to 190 grams (Fig. 7).

Biswell and Weaver (1933) found not only that the total dry weight produced from sods frequently clipped after transplanting ranged from 13.1 to 47.5 per cent of that of the same species of prairie grass unclipped after transplanting but also that the clipped plants failed to produce new rhizomes and many of the old ones died. The length of the roots was greatly decreased, and the relative production of roots was more greatly reduced than that of tops. Plants weakened by repeated clipping renewed growth slowly if at all after the sods were frozen, although the controls made an excellent development. They give a comprehensive review of the literature.

McCarty (1938) has shown that the "Initial growth of herbage in spring is made at the expense of the carbohydrate accumulations stored in the basal organs during the preceding season. Concentration of carbohydrates in both herbage and basal organs of the plant is inversely related to the rate of herbage growth. This relationship is maintained throughout the entire annual cycle of growth. The accumulation of carbohydrate stores is delayed, therefore, until most of the annual herbage growth is produced." It is well known that all of the stored food is not ordinarily used in normal early growth of

perennial grasses. But if the new growth is removed by early grazing or clipping there results a diminution in the reserve food; a second close clipping may further deplete the supply. Thus, the progressive decrease in yield of the closely clipped quadrats and the final death of many plants may be readily understood.

SUMMARY

The yields from the several stations during the three years are shown in Table 5. From a survey of these data a number of conclusions may be drawn. The season of 1935 was the best for the growth of grasses, 1933 being intermediate, and 1934 distinctly the poorest.

TABLE 5.—Total production in grams of dry matter from the control and clip quadrats at the several stations, and percentage yield of clip quadrats in terms of yield of controls.

Species and criteria	Control '33	Clipped '33	Control '34	Clipped '34	Clipped '33+'34	Control '35	Clipped '34+'35	Clipped '33+'34+'35
Little bluestem	348.0	385.3	135.5	170.2	68.7 1	588.8	319.8	186.0 2
Percentage of control	111	126	51	54	32
Big bluestem	668.3	407.8	139.7	158.1	100.2 3
Percentage of control	61	113	72
Mixed bluestems	340	332.9	143.1	139.5	68.1 4	426.6	244.5	189.5 5
Percentage of control	98	98	48	57	44
Mixed bluestem pasture	248.0	246.8	97.5	39.5
Percentage of control	99
	Control on upland Short grasses	Clipped	Control on lowland Short grasses	Clipped	Control on lowland Bluegrass	Clipped		
Yields in 1933	181.7	192.4	212.2	276.6	263.0	274.8		
Pct. of control	106	130	105		

1. Yield only 40 per cent as great as from quadrats clipped one year.
2. Yield only 58 per cent as great as from quadrats clipped two years.
3. Yield only 63 per cent as great as from quadrats clipped one year.
4. Yield only 49 per cent as great as from quadrats clipped one year.
5. Yield only 77 per cent as great as from quadrats clipped two years.

Total yields of the quadrats cut at frequent intervals for the first time exceeded those of the single yield from the controls at 4 of the 6 stations in 1933. With little bluestem the excess was 11 per cent; at the upland short-grass station, 6; at the lowland short-grass station the increase was 30 per cent; and at the bluegrass station, 5. On the hillside in prairie of little and big bluestem type, a slight decrease occurred. In the big bluestem, a decrease of 39 per cent was determined. This resulted undoubtedly from the heavy flower-stalk production of the controls. Similar results were obtained from the quad-

rats first clipped in 1934. Little bluestem yielded 26 per cent more than the control, except where it was intermixed with big bluestem where it yielded 2 per cent less. Big bluestem, failing during this drought year to produce flower stalks, yielded 13 per cent more from the several clippings than from the single harvest.

Quadrats closely clipped for two seasons always gave lower total yields than a single clipping of the controls. In little bluestem the yield averaged 49 and 46 per cent less, in big bluestem 28 per cent less, and in mixed little and big bluestem 52 and 43 per cent less than the controls.

Yields from quadrats frequently clipped during two years were likewise much lower than from those similarly clipped for only a single year. In little bluestem the former yielded 60 per cent less, in big bluestem 37, and in mixed bluestem 51 per cent less.

At two stations, clipping was continued in the same quadrats for a period of three years. Compared with the controls, yields were 68 and 56 per cent less, respectively, in little bluestem and mixed bluestem types. When the yields are compared with those from quadrats frequently clipped for two years they are found to be 42 and 23 per cent less, respectively. Thus there is a rapid decrease in yield following too close utilization of pasture. The plant parts underground also deteriorate. Decrease in dry weight varied from 33 to 41 per cent after two years of close clipping, and was 57 to 59 per cent in mid-summer of the third year.

Where upland, little-bluestem prairie degenerated into pasture of the short-grass type, the seasonal yield was reduced to 52 per cent when the vegetation was removed only in fall. Where it was removed by frequent clipping, as in close grazing, the yield was only 50 per cent as great.

A single year of close grazing reduced the next year's yield of mixed bluestem prairie to 74 per cent. When this was followed by a second year of clipping the yield decreased to only 29 per cent of that of virgin prairie similarly clipped.

Where big bluestem degenerated to short-grass pasture the forage yield measured once in fall was reduced to 32 per cent. Where clipping to simulate close grazing was practiced, the yield was decreased to 68 per cent. Similar comparisons of yield of big bluestem and bluegrass pastures on low ground gave a reduction to 39 and 67 per cent, respectively. Since the yields from short-grass and bluegrass are for a single year only, because of severe drought, they are merely indicative.

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Fire in Land Use and Management¹

Herbert C. Hanson

Causes of Fire

In ecology fire is usually classified as a biotic factor because man is in most cases, the causative agent. It should also be classified with climatic factors because fire may be due to lightning and less frequently to spontaneous combustion, meteors, materials ejected from volcanoes, and by friction developed by avalanches, falling boulders, and possibly by tree branches or bamboo canes rubbing against each other in the wind.

Averill and Frost (1933) have named the following causes of man-made fires and the percentage for each cause in the timberlands of Massachusetts from 1926 to 1931 inclusive; smokers 35.0 per cent, railroads 25.0, children 11.0, brush burning 10.0, incendiary 6.4, rubbish burning 5.1, miscellaneous 4.0, grass burning 2.0, campers 0.7, dwellings 0.6, fishermen 0.2. Of the total number of 2230.4 fires during this period, lightning started only 0.4 per cent. For Minnesota forests Mitchell (1927) has contributed the following table:

	1916-20	1921-25
Land clearing -----	29.7%	26.3%
Railroads -----	24.7	20.1
Campers and smokers -----	15.4	23.2
Miscellaneous -----	30.2	30.4
	100.0%	100.0%

Lightning was responsible for less than 1 per cent and incendiarism for about 3 per cent. In California, however, lightning caused about 41 per cent of the 10,476 fires on and adjacent to 12 timbered national forests from 1911 to 1920 inclusive. Campers were responsible for about 20 per cent, incendiaries 17, unknown 6, brush burning 3, miscellaneous 4, lumbering 6, railroads 3. The following data are available for forest fires in Michigan (Mitchell & Sayre).

	1918-1922	1923-1927
Land clearing -----	28.3%	25.0%
Railroads -----	20.1	19.4
Campfires -----	26.5	17.0
Smokers -----	3.1	24.1
Incendiary -----	1.8	3.6
Lightning -----	4.6	1.2
Lumbering -----	15.6	1.2
Miscellaneous -----	21.4	8.5
Unknown -----		27.82
T o t a l -----	100.0%	100.0%

¹ One of the papers given as the joint symposium of the American Association for the Adv. of Science and The Ecological Society of America at Ottawa, Can., June, 1938.

² Unknown prorated among other causes, railroads excepted.

In the South "most of the woods fires are started by hunters, smokers, stockmen, and others upon lands which they do not own. To these fires are added the fires escaping from railroad engines, logging operations, field clearings, and "warming fires." There has thus grown up the belief in many quarters that woods burning is as inevitable as the seasons. Landowners feel that it is hopeless to try to keep fires from their land. So they become, in their helplessness, advocates of spring and fall burning. And one of the chief reasons they advance is that spring and fall burning is a means of defending their property against fires set by others" (For. Serv. 1929). Pitt and Bogert have summarized the causes of 150,000 forest fires occurring annually in the United States as lightning, 8 per cent, and man, 92 per cent. Smokers and campers top the list of man-caused fires with 31 per cent, incendiaries 26, and negligence in brush-burning, logging and railroading and the remaining 35 per cent.

Spontaneous combustion probably occurs only rarely. Tingey (1933) reports such a cause in Canada thistle plots, located in undergrowth of dry bluegrass in Utah. The fire started following treatment with Atlacide and a sudden rise from 65° to 75° F. and a fall in relative humidity from 66 to 31 per cent. Viosca (1931) witnessed spontaneous ignition of a dry coastal marsh near Mandeville, Louisiana, when the temperature was 100° to 104° F. and the wind movement was estimated at 20 to 25 miles per hour. Due to the high combustibility of the marsh material and the wind velocity the fire was beyond control when reached. Other materials reported to have ignited spontaneously are damp hay, freshly mown grass, and charcoal. Looker (1937) estimated that spontaneous combustion is responsible for about \$30,000,000 damage to farm property annually in the United States.

Ecological Effects of Fire

In evaluating the advantages and disadvantages of fire in specific instances of land use and management full consideration should be given to all of the possible ecological effects of fire. Similar to the use of other drastic ecological tools, such as poisoned bait and spraying materials, the expected beneficial effects must be carefully compared to expected harmful effects. Decision regarding the use of fire in any specific case will be scientific, and practical, insofar as it is based upon thorough analysis of the ecological effects. The decision is not easy to make because data regarding these effects are woefully scarce. Much of the literature regarding fire indicates merely that since plant materials and organic matter are destroyed the consequences must be bad. Such reasoning is deficient. Exact data regarding the changes produced by the fire as well as the effects upon consequent plant and animal life on the burned area are needed. It is not intelligent to assume that since fire is injurious in some cases that it is always undesirable. The use of strychnine is not prohibited because in some cases it has caused greivous consequences.

The following list of classes of ecological effects of fire is probably very incomplete but it may prove to be serviceable not only in evaluating the use

of fire in particular cases but also in aiding in the formulation of research projects.

1. Burning causes partial or complete destruction of plant and animal life, as well as dead vegetation cover.
2. Burning causes modification of atmospheric factors; light, wind, precipitation (rainfall interception.)
3. Direct effect of the temperature of the fire upon the soil, as organic and mineral contents, structure, texture, animal and plant life in the soil.
4. Effect of destruction of plant cover upon consequent soil moisture, wind and water erosion, mineral content, biotic processes in soil, pH, etc.
5. Effect of fire upon consequent plant and animal succession, relation of fire to aiding establishment of early invaders as Lodgepole pine.
6. Effect of subterranean fires upon rock formation and topography.

1. PARTIAL OR COMPLETE DESTRUCTION OF PLANT AND ANIMAL LIFE, AND COVER

Amplification of these classes or groups of effects will clarify them and probably aid in making them more useful. In regard to the burning of vegetation it is well known that some species are more resistant to burning than others. In a severe forest or brush fire, or in repeated burnings on the same area, resistance to fire may be of no avail, but in lighter burnings, and usually in grasslands, fires are highly selective in their effects.

The burning of grasslands has been widely practised and much discussed but carefully investigated in only a few cases. Aldous (1934) by means of experimental plots on bluestem pastures in Kansas determined that "Burning decreased the yield of the mature vegetation. The yield was least on the plots burned in the late fall. The plot burned in the early spring was next, followed by the plot burned in medium spring," and finally the plots burned in late spring. "Burning had little effect in controlling weeds and brush unless it was done in the late spring or after April 20. . . . If the low point in the organic food reserves is later than May, as is true of sumac, burning is not an effective means of eradication." Burning increased the leafiness and protein content of bluestem in the first part of the growing season. Plots burned in late fall and early spring had a greater number of plants than the unburned plot. Little bluestem increased in plots burned in late fall; coarser grasses, as big bluestem, increased on those burned in late spring; Kentucky bluegrass increased on all unburned plots and decreased or was eliminated on all burned plots. Burning stimulated early spring growth.

The burning of broom sedge in the southeastern states apparently requires further research but there are indications that in West Virginia burning the dry grass in the spring tends to kill more desirable species and at the same time increases the growth of broom sedge in early spring (Smith 1938). In South Africa, however, Phillips, E. P., (1931) states that the veld, if left

alone for a number of years becomes rank and coarse, depreciates in grazing value and the dead grass culms do not readily turn into humus. The best grass, such as rooi-grass, gradually dies out and is replaced by coarser grasses belonging to the tribe Andropogoneae. Fire may also be a factor in the elimination of certain growth forms, in addition to maintaining an "open" or savannah condition on vast areas, (Phillips, J. F. V. 1930). Burning coarse grasses in order to get rid of the dry, unnutritious growth of the previous season and to secure more palatable forage is widely practised in other parts of Africa, Madagascar, and South America but little research has been done (Jacks and Whyte, 1938, and Myers, 1936). In Western North Dakota the author has observed that burning might improve the grazing value of areas of little bluestem and sand grass which ordinarily have very low palatability, but it is more desirable to retain such vegetation as reserves against drought. In southern Mississippi Wahlenberg (1937) reports on the basis of an experiment started in 1923 that the two dominant native grasses, *Andropogon scoparius* and *A. tener*, were thinned out severely by the smothering effect of dead vegetation which accumulated under fire protection but that on the areas burned annually the original proportion and density of native grasses were more nearly maintained. He states further that for a period of 11 years the cattle on the burned area consistently showed better gains, namely 69 pounds per head for the grazing season on the unburned pasture and 101 pounds on the burned pasture. Chemical analysis showed less protein, lime, and phosphorus in the green grass from the unburned pasture.

Serious damage to range land in Nevada caused by grass fires is emphasized by Fleming (1938). *Bromus tectorum* has invaded wide areas and when this grass has grown to a height of 10 to 18 inches it constitutes a serious fire menace from July through September. Fleming reports thousands of acres of sagebrush land that have lost most of their original vegetation cover as a result of fires. He reports open yellow pine stands destroyed or seriously injured as a result of fires started from dry *B. tectorum*.

The ecological effects of fire on woody plants are better known. Research is continuously yielding much-needed additional data for land management. The Michigan Forest Fire Experiment Station (Anonymous, 1936) showed, that although spring fires in sprout oak stands are believed to cause but little direct damage, practically all trees and sprouts under 4 inches were killed back, all jack pines were killed, oaks and aspens increased greatly, aspen replaced oak as the dominant, and all of the larger oaks surviving were severely damaged. Dominance by the aspen is due as Kittredge (1938) has pointed out to its promptness in producing off-shoots following fire. Most of the aspen stands in Minnesota and Wisconsin have originated in this way. Lutz (1934) as the result of a careful analysis of the role of fire in the pitch pine plains in southern New Jersey gives as the chief reason for the stunting of trees that, since fires burn over the plains on an average of once in 8 years, shoots are destroyed before they attain much height and this leads to so many shoots that only rarely can one grow into normal size. Fire, evidently, has been a factor in molding the life-form of various species. According to Bauer (1936)

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"All investigators agree that fire has contributed much to the present appearance of chaparral. It is believed to have affected the stature, form, and xeric characteristics of the plants. A number of species respond to repeated fires by developing just below the surface of the ground, large, tuberous platforms, or irregularly shaped masses of woody tissue from which numerous stems may arise." The heterogeneity of many forest and shrub stands is attributed to the presence of fire by various writers. "A fire often does not sweep the area clean, but burns irregularly, leaving islands in the midst of the burned area. . . . The new growth may be somewhat different from that of the unburned island and thus, make for a lack of uniformity in the vegetation after recovery from the fire is complete."

Many observations have been made regarding fire sensitivity of woody species. Daubenmire (1936) reports that the hard maple followed by the red maple are the most fire susceptible species in the Big Woods in south-central Minnesota. Stallard (1929) considered the white oak as the most fire-sensitive species of oak in Minnesota. According to Pessin's observation (1933) in the Lower Gulf Coastal Plain, the scrub oak as turkey oak, post oak, and blue jack oak are rarely killed by surface fires. The stems alone may be killed or badly injured, but several stems tend to replace each one destroyed. This produces keener competition for water between oaks and pine seedlings, and under conditions of periodic burning coniferous forest may result, but complete fire protection appears necessary for a deciduous climax forest to develop. Other fire-sensitive species are hemlock, white pine, beech, and juniper (Bromley, 1935). It is well known that the long-leaf pine, western yellow pine and sugar pine are highly resistant. The capacity of huckleberry to produce sprouts following burning has been utilized to produce new shoots and thus increase yields (Lutz, 1930). Various writers (Show & Kotok, 1929, and MacDonald, 1938) emphasize that young trees and seedlings are particularly sensitive to fire, especially ground fire, because the bark is thinner and the buds and leaves are more exposed to injury. Furthermore the loss of young reproduction endangers continuance of the forest. Another serious aspect of forest fires is that the immediate effect of the fire is to kill all or many of the live trees. This dead material together with inflammable vegetation such as dry grass which may appear later on the burned area leads to a greater fire hazard and possibly to a more destructive fire than the first one (Larsen, 1929, and Korstian, 1937).

Fire directly destroys animal life and alters conditions so that many previous inhabitants are replaced. The animals that are destroyed or migrate away, due to the fire, or that invade following the fire are mostly beneficial, but some species are harmful. The two following quotations well express some of these fire relations.

Grass fires, which are of regular occurrence over most of the African savannas, undoubtedly play an important part in influencing both plant and animal distribution. Ground-nesting birds in particular, must regulate their breeding activities as much in accordance with the periodic recurrence of fires, as with the seasonal cycle of rainfall. Insect life, perhaps the chief food source of most savannah birds, is driven off or destroyed by these fires and, for a period of varying length, these savannas become

little more than a charred wilderness with scarcely a trace of food or cover for the avifauna (Bowen, 1933).

Fire is also well exemplified in the Spruce Forest Reservation near Carberry, Manitoba, where former extensive tracts of prairie are now covered with young aspens. In later years the fire hazard has increased, for, with frequent fields and roads, the danger of large fires has been so reduced that people have lost all fear of them. In fact in the spring, after the snow has gone and the grass is as dry as tinder, people seem to develop a perfect mania for setting fires. The fires sweep into the groves of aspen, killing many of the trees and so weakening others that they are soon killed by the heart rot, *Fomes ignarius*, other fungi and wood-boring insect larvae. On the other hand, certain plants are benefited by periodic burning, particularly the raspberry, *Rubus idaeus aculeatissimus* R. & T., the fire weed, *Epilobium angustifolium* L., and many asters, sunflowers, and goldenrods. Some insects are killed by fires, but the greatest danger is to the birds whose nests and nesting sites are destroyed (Bird, 1930).

Fire has been much used to control pests by burning brush as in the case of the dreaded tsetse fly in Africa and by burning crop residues and debris for such insects as the European corn borer, cotton boll weevil, true and false chinch bugs, pea aphid, borers, gall formers, flea larvae, and sorghum webworm (Swynnerton, 1936; Munro, 1938; Reinhard, 1938; and Sturgis, 1932). In Wisconsin Graber (1926, 1936) has applied fire in a most interesting manner in the renovation of weedy, infertile, grub infested bluegrass pastures. The bluegrass is weakened by burning off the old grass and weeds in the spring after growth has started, the grass recovers slowly, fertilizers may be applied, the sod is disked, seed of legumes is planted, and due to decreased competition the legumes become established readily. Later the bluegrass is greatly benefited by the legumes. The legumes, as sweet clover, alfalfa and red clover are repellant to the egg-laying parent (June beetles) of the white grub. In one treated pasture of 22 acres no grubs could be found, while on an adjacent untreated pasture they were present at the rate of 140,000 per acre. Bishopp (1938) urging the need of cooperation among scientists, points out that too often in planning crop rotations insects are not given sufficient consideration.

Show and Kotok (1925) describe an apparently general effect of fire upon subsequent insect infestation. Small beetles attracted by the scorched needles or burned trunks, attack first weakened trees and later the more vigorous trees. This results in an epidemic on the burned area of some 3 to 5 years in duration, during which much damage occurs. Pearson and McIntyre (1935) state that although 3 species of beetles are attracted to fresh ponderosa pine slash in the Southwest and may enter and kill nearby standing trees only exceptionally it is necessary to dispose of the slash for this purpose.

The destruction by fire of plant accumulations (litter, debris, crop residues, etc.,) has many ecological implications (Munns & Simms, 1936). Morgan and Lunt (1932) measured the amount of leaves, twigs, bark, etc., upon the soil surface of a well-stocked, 27-year-old white pine plantation at 2,000 to 3,000 pounds per acre. Sturgis (1932) calculated that on 184,000 acres of sugar cane harvested in Louisiana in 1930 there was an average of 8.3 tons of "trash" (leaves and upper part of stalks) per acre. In Iowa, dry, wind-blown corn stalks vary in weight per acre from 0.5 to 1.5 tons (Davidson and

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Collins, 1930). Stoa (1938) calculated the yield of straw from various crops in North Dakota as, hard red spring wheat 1700 to 2000 pounds per acre, durum wheat 1800 to 2400, barley 1400 to 1900, oats 1600 to 2100, and flax 1000 to 1500. These materials harbor a varied fauna and flora; they modify factors such as soil and surface temperature, humidity, reception and penetration of precipitation, evaporation of soil moisture, runoff and erosion; they influence directly and indirectly soil fertility, soil structure and soil development; and they may interfere with man's cropping operations. Advantages in burning sugar cane trash are that the large bulk handicaps field tillage, the material decomposes slowly under dry conditions, thus forming a fire hazard for the subsequent crop and it may serve as breeding material for injurious fungi and insects. An important advantage in plowing under the trash is that the crop needs the residues to maintain the soil in high fertility, especially the nitrogen content (Sturgis, 1932, and Lee, 1938).

It is doubtful whether the benefits secured in destruction of weed seeds by burning of plant residues justifies the consequent loss in fertility and exposure of soil to wind and water erosion and runoff. A case of stubble burning is reported by Starch and Kurtz (1929) as reducing the number of weeds per acre on burned ground to 88,000 compared with 144,000 on the unburned. Weeds an inch or more in height had to be exposed to a hot blaze for about a minute before they were killed, but those just emerging from the ground were killed more easily. Stubble burning had no effect on larvae or eggs of insects, nor on weeds covered by even a small amount of soil. Tests are being started at the Northern Great Plains Field Station near Mandan, North Dakota, to determine if top burning of weeds, as a method of fallowing, is cheaper and less conducive to wind erosion than cultivation. Forest litter furnishes a storage reservoir and later, ideal germination conditions, for seeds of numerous valuable species such as conifers, the chestnut oak (Barrett, 1931) and others. Fire not only destroys many of these seeds but also the favorable conditions. Other species, as the lodgepole pine, are favored by the fire, in that the cones lie dormant in the duff, or remain on the branches until overwood stand is removed (Haig, 1932). Slash disposal following lumbering operations has received much attention and, as Pearson and McIntyre (1935) have emphasized, one method cannot be used uniformly over a large area. The method must be adapted to meet conditions on the particular site because the interrelations of slash to fire hazard, tree reproduction, propagation of injurious insects and fungi and accumulation of ungrazed grass vary from place to place.

Dachnowski-Stokes (1937), laudably calls attention to the 1930 U. S. Census which shows a "dismaying total" number of acres in drainage enterprises and percentage of land delinquent in drainage taxes and in addition *unimproved* and *idle*, in Florida, Minnesota, Wisconsin, Oregon, and other states. Before peat is subjected to fire hazard by drainage or is purposely burned, careful consideration should be given to the inherent value (Dachnowski-Stokes, 1933) of this material which has required thousands of years for its accumulation. Sears and Janson (1933) estimated that the mean rate of peat

accumulation during the past several thousand years in the Great Lakes area as 20 to 30 years per inch. Other estimates cited by these writers range from 2 to 1650 years per foot. Dachnowski-Stokes (1935) states that "the highest practical value (of peat areas) is their protective function in conserving precipitation, storing water supplies, checking floods, erosion and silting, and maintaining a sufficiently high water table in surrounding land." Moss peat has an absorptive capacity of about 5200 tons of water per acre-foot of dry matter; reed and sedge peat 4100 and 3500 tons respectively. These quantities amount to 167,000 cubic feet per acre for moss peat; 131,000 for reed peat, and 112,000 for sedge peat and are equivalent to rainfalls of 46, 36, and 31 inches respectively. Dachnowski-Stokes concludes that because of this great absorbing and retaining capacity peat areas are very important in storage of water and in mitigation of severe floods and they should, therefore not be burned, drained excessively, or otherwise interfered with in their normal development and protective function. The Ecological Society of America in its annual business meeting in 1934 urged similar use of peat lands by the following resolution which was adopted unanimously.

That we endorse most fully all movements for the preservation of natural areas for purposes of study, realizing that the importance of such preservation needs to be made known both to the scientific world and to the general public. Peat deposits, lake and marsh areas of all sorts are valuable in helping to maintain the water table which has been so greatly lowered in many places during the past few years. Peat land should be protected from burning and over-drainage. We urge that all government agencies cooperate in conservation of peat resources and in the preservation of marsh areas as well as extensive areas of forest and grassland.

According to the 1937 report of Governor's Commission on the Conservation of Florida's Natural Resources (Anonymous, 1937) 20 to 25 per cent of the 2,000,000 acres in the 4,500,000 acres in the Everglades Drainage District "has been rendered totally worthless for agriculture" because of denudation of peat and muck by fire. This represents a loss of \$40,000,000 at a valuation of \$100.00 per acre. The report adds that the remaining 1,600,000 acres will shortly go the same way unless decisive steps are taken to control the fires which destroy the peat to a depth of 2 or 4 inches to 3 or 4 feet in a single burn. Clayton (1936) has called attention to the reduction in elevation of peat areas in Florida by fires, which may cause increase in lime or alkalies in the surface layer. Two essential features in reducing the number of fires is the prohibition of alligator killing because the hunters start fires so as to deprive alligators of protective vegetation and to reduce fire hazards by restoring water to areas now drained but not used in agriculture. The latter plan would not only reduce inflammability of vegetation but raise the water-level of underground waters which have been severely over-drained and may reduce frost damage to crops on lower east and west coasts.

Penfound and Hathaway (1938) described the serious consequences of fires started mostly by muskrat hunters, in decreasing the elevation of Louisiana marshes by as much as 1 to 3 feet, causing reversion to moister, and possibly alkali, conditions, changes in vegetation and delaying succession.

Jacot (1936) has performed valuable service in pointing out the need for good vegetation covering as a condition for the extremely important activities of the generally distributed Oribatid mites, minute earthworms, spring-tails, and ants in improving and maintaining the tilth and fertility of the soil. The effects of fire upon these animals which spend all their lives in the soil have not been studied at all adequately. It is urgent to secure more research data on the relation of fire and other factors to these animals as well as those which spend only part of their time in the soil.

Fire has been widely used as a sanitation measure in the control of plant disease. Burning of diseased plants or parts of plants, of disease-harboring plant debris, and of plants which may be alternate hosts to a disease organism or which may protect the insect carrier of the disease, is recommended for the control of diseases of many economic plants (Smith, 1937, and Heald, 1933) such as virus diseases in cucumber, cotton, lily, strawberry, peach (phony disease), raspberry, tobacco, banana, rice (dwarf disease), smut and dry rot of corn, early and late blight of potato, ergot in grasses and grains, anthracnose in currants, white rust of crucifers, and rots in trees. On the other hand fire is claimed to be responsible for some diseases as rots gaining infection in trees through fire wounds. Fritz (1932) indicates that 90 per cent or more of "dry rot" infections in the California redwood region is due to fire, and Show and Kotok (1925) state that nearly all serious infections of the white fir in California were traceable to fire wounds.

In many cases rotation of crops can perhaps be substituted for fire so that soil fertility will also be improved but much research is needed as a foundation for better practises. Our knowledge is as yet very inadequate regarding the life histories and environmental relations of disease-producing organisms and insects, effects of plant residues upon the soil and how these effects may be modified by tillage operations, kinds of rotation, and applications of various chemicals. The soil chemist, bacteriologist, entomologist, zoologist, and mycologist must join hands with the agronomist and plant pathologist in solving the intricate problems involved. A recent paper by Rogers (1937) indicates that 4-year rotations of non-susceptible crops (corn, sorghum, oats or wheat) with cotton showed consistent reduction in cotton root-rot but that 3-year rotations (corn, oats, sorghum, or fallow) were not effective. In two 4-year rotation tests during the rotation period, 1928-36, the average reduction of the disease was 57.5 per cent as compared with the continuous cotton field. Devices on machinery, as trash guides, which handle residues better, are being developed. Combines return the straw to the land, and tools such as the one-way disc and Killifer chisel turn only a portion of the straw, the remaining part projecting above to catch blowing soil and snow (Harper, 1932, Cole and Morgan, 1938). Eisenmenqer (1938) indicated that timothy and corn were unsatisfactory for rotation in growing tobacco, but ragweed, horseweed and tobacco desirable. He suggested that this might be due to the higher values of lignin, pentosans, high carbon-nitrogen ratios and subsequent low tendency to protein decomposition in the soil of the residues of unsatisfactory species.

Waksman and Gerretsen (1931) report that lignin in oat straw decomposes fairly rapidly at 37° C. (98° F.) but are nearly preserved at 7° C. (44.6° F.) They also state that the addition of available nitrogen hastens decomposition of residues as a whole, especially hemicelluloses and cellulose, but it has very little effect on lignin.

2. MODIFICATION OF ATMOSPHERIC FACTORS

Burning grass in which long leaf pines are growing appears to be the best measure for controlling brown-spot needle disease which seriously retards growth of longleaf pines on grassy areas not burned. The grass apparently furnishes optimum conditions, especially in humidity and light, for infection. Fire is one of the factors responsible for difficulties in controlling white pine blister rust. Cooper (1922) showed that gooseberries, the alternate host of this disease, produced 22 per cent greater leaf area in the open than in the closed forest, thereby explaining in part why gooseberries are common in early stages following fire. The gooseberries in the open localities were more heavily infested than in the forest; 59 per cent of the open localities showed infested gooseberries compared to only 25 per cent of the localities in the climax forest. In an infested region any initial cause, therefore, as fire, that produces openings followed by gooseberry invasion, definitely favors the spread of white pine blister rust.

3. DIRECT EFFECT OF TEMPERATURE OF FIRE UPON THE SOIL

There are many records available on the direct effect of the temperature of fire upon the soil. Heyward (1938) recently published some excellent data on 44 fires in longleaf pine forests in Florida and Mississippi. His chief conclusions are as follows:

These records showed that, at a depth of $\frac{1}{8}$ to $\frac{1}{4}$ inch, temperatures only slightly higher than those of the air and ranging up to 274° F. occurred . . . the majority ranging from 150° to 175° F. These temperatures generally persisted for 2 to 4 minutes, after which they declined rapidly. . . . The maximum of 65 temperature records for the $\frac{1}{2}$ -inch depth was 195° F., this accompanied a temperature of 274° F. at the $\frac{1}{8}$ -inch depth. . . . Only slight increases in temperature were recorded at a depth of 1 inch. For one fire, obtained by piling and burning pine straw on the soil, a maximum temperature of 313° F. at $\frac{1}{8}$ -inch was accompanied by maximum temperatures of 178° and 153° F. for the $\frac{1}{2}$ -to 1-inch soil depths, respectively. . . . A review of literature reveals that numerous researches have shown consistently higher concentrations of soluble salts and ammonia in soils heated up to 212° F. than in unheated soils. Heating to higher temperatures resulted in decreased fertility. The above findings indicate that the heat from the majority of forest fires in the longleaf pine region is insufficient to impoverish the soil, and that the slight heat which enters the soil during these fires may even favor plant nutrition.

Experiments with fire from stubble-burning machines at Swift Current, Sask., Canada, showed that the temperature at 0.25 inch deep in the soil was raised only 1 to 3 degrees and that weed seeds on the ground are not affected by the heat unless entirely exposed to the fire (Starch and Kurtz, 1929). According to Levy (1937) fire is one of the chief tools used in New Zealand to convert its rain forest into grassland; 12,000,000 acres having been success-

fully converted and several million more are awaiting development. After underscrubbing, the trees are felled by axe during the winter and early spring. On a favorable day during a dry spell in the next summer the fire is started. A steady, hot fire, or "white burn" is desired so that all fallen timber, leaf mold, seeds and fern spores will be destroyed leaving a white ash. A black burn does not destroy the seeds and spores, and interferes in development of the grassland. Sowing of turnips may precede planting of a grass and legume mixture. The new burn is stocked with sheep and cattle about 8 weeks after sowing. It is essential that the stock graze and tread all parts of the burn so that fern and scrub growth will be destroyed and ecological conditions be made favorable for grass instead of forest. Temperatures caused by slash fires in the Douglas fir region near Carson, Washington, reached 1841° F. just above the duff surface and 608° F. 1 inch below it (Isaac and Hopkins, 1937).

4. EFFECT OF DESTRUCTION OF PLANT COVER UPON SOILS

Many observers have reported washing away of great quantities of the fine, loose soil and ash left on steep slopes following fire. This fine silt may later be deposited in reservoirs, in orchards, or highways and railroads causing considerable damage. Runoff is often greatly increased and revegetation of the burned slopes is delayed in relation to the amount of topsoil washed away (Munns and Simms, 1936.) Skutch (1929) reported loss by fire of all soils above granite rocks on Mt. Desert Island, Maine, leaving dead trees propped up several inches above the rock. Only through the agency of plant succession, requiring perhaps centuries, can the soil be rebuilt. In the Cranberry Lake Region of the Adirondack Mountains Young (1934) reported that the thickness of the humus layer varies from 1 inch in burned areas to 26 inches in old white pine stands. Jacks and Whyte (1938) give the following striking picture regarding the effects of uncontrolled burning on erosion and social conditions in North Bengal and Assam.

The *taungya* system of shifting cultivation (felling a hillside, burning, cropping for 2-3 years and leaving for 30-40 years) has been practised for centuries, and the long rest enabled the land to recover, as the tree growth is rapid. Owing to disease and feuds, there was always sufficient land for the population without undue pressure on the forests. The result of British rule has been to increase the population and correspondingly to reduce the rest period. The consequent erosion has reduced stream flow, and shortage of water has forced the villagers to make new villages on hitherto virgin land. The main rivers in the plains are now frequently in a state of violent flood. 'In many parts of East India the extent of new shifting cultivation has to be seen to be believed; during the day there is a thick canopy of smoke over the whole country, while at night, looking up to the hills from the plains, the lights of fires can be seen as far as the eye can reach.'

Review of considerable recent literature and much correspondence have yielded but few research data on the physical and chemical effects of burning under known circumstances. There are numerous generalizations but much remains to be learned by research to determine whether, under the conditions prevailing in the locality, the effect of fire on soils are beneficial or detrimental.

Alway and Rost (1927) made extensive soil studies following serious fire, in northern Minnesota on October 12, 1918. Conclusions from their analytical data are that "there is no evidence that the fire caused any significant change in chemical composition or physical properties of the soil below the surface layer of organic residues, even where this was entirely burned off. The lime, phosphoric acid and potash of the leaf-mold would suffer no loss by burning and much would be left in a more immediately available form." In pot experiments with barley, oats, and red clover they found that both leaf-mold and ash from burning the leafmold increased yields in all cases and that burning all or only half the leafmold gave lower yields than using it unburned.

Isaac and Hopkins (1937) conclude from research studies in Douglas fir soils near Carson, Washington, that.

The usual heavy slash fire results in almost complete destruction of the duff layer. Involved in and associated with this destruction, on the particular area studied, were the following: (1) a loss per acre of 25 tons (89%) of the organic matter contained in the duff; (2) a change in duff reaction from a highly acid condition (pH 4.95) to an alkaline condition (pH 7.6); (3) the escape of approximately 435 pounds of nitrogen per acre; (4) an increase in the supply of plant nutrients available in the surface soil. This resulted from deposition at the surface, in highly soluble form, of a part of the nutrients present in the duff, which in the absence of fire would probably have become available gradually, over a long period of years. Serious subsequent losses by leaching appeared probable; and (5) an indicated loss of a considerable part of the mineral nutrients contained in the duff, presumably carried off in smoke.

The action of slash fire upon the surface zone of the mineral soil causes some dehydration of secondary minerals, colloidal breakdown, change from a favorable to an unfavorable structure, and reduction of moisture-holding capacity to a point at which seedling survival is seriously affected.

Unburned-soil conditions, in which normal quantities of plant food are made available gradually throughout the regeneration period, appear to be more favorable to Douglas fir regeneration. For this reason, and because of the adverse after-effects of fire on surface-soil temperature and soil moisture, two critical influences on initial establishment of Douglas fir, this study has led to the conclusion that the harmful effects of the ordinary slash fire more than outweigh any beneficial effects it may have on the productivity of Douglas fir forest soil. The study indicates further that the harm done is roughly proportional to the completeness with which the fire consumes the duff and the organic matter in the surface soil.

Wahlenberg (1937) in longleaf pine areas in southern Mississippi found that soil organic matter and nitrogen content were slightly less on unburned soil due probably to reduction of grass roots and decreased stand of legumes on land not burned. The soil on burned areas was more compact. Heyward and Barnette (1934) concluded from an intensive study in longleaf pine forests extending from South Carolina to Louisiana that soils (upper 4 to 6 inches) subjected to frequent fires were consistently less acid, had higher percentages of replaceable calcium and total nitrogen, and indications of larger amounts of organic matter than unburned areas. They emphasize that before final conclusions can be made regarding the physiological effects of fire on tree growth that many factors remain to be measured and carefully evaluated. Greene (1935) reported the following results from an 8-year study of annual grass burning in longleaf pine forest in Mississippi.

Whether plant debris was burned in place on top of the soil or was left to rot in

place on top of the soil apparently had no direct effect on either the organic matter content or the nitrogen content of the soil. In both cases, the organic matter and nitrogen above ground were largely lost to the soil and the nonvolatile mineral fertilizing elements were returned, leaving organic matter and nitrogen increases to be influenced by the amount and composition of decaying plant roots. . . .

The quantity of forage growth on the ungrazed burned areas at the end of the period was more than double that on the unburned areas. The additional quantities of plant roots decaying in the soil on the burned areas apparently account for the increase in soil organic matter to a depth of 6 in. The increased growth on the burned areas of native legumes, their ability to take nitrogen from the air, and the additional growth of other plants which take up soluble forms of nitrogen and prevent leaching apparently account for the increased amount of soil nitrogen. The increase in organic matter and nitrogen on the burned areas was reflected in the higher crude-protein content of the principal forage grasses that grew on burned areas as contrasted with the unburned.

Annual burning returned the nonvolatile fertilizing elements to the soil immediately. This was shown in the analyses of both the soil and the forage growth. The increased organic matter and nitrogen in the burned-over soils was reflected in an increased number of soil micro-organisms. The accumulation of plant debris on top of the soil did not materially increase the soil moisture in spite of the fact that much greater amounts of water were required to support the extra forage growth on the burned-over soils. Organic matter on top of the soil absorbs a portion of the rainfall, which is thus prevented from reaching the soil for the use of growing plants.

Heyward and Tissot (1936) ascribe the more porous and penetrable, better aerated soils of unburned longleaf pine forests as compared with those of burned forests, to the diversified, active fauna present in greater abundance in unburned soils. The A° horizon of the unburned soil had about 5 times as many microfaunal forms (chiefly mites) as that of the burned soil and the upper 2 inches of the mineral soil had 11 times more such animals. Auten (1934) published data showing that yellow silt loam in Illinois and cherty loam in Arkansas in burned oak woods had much lower water absorptive capacities as compared with similar soils in unburned oak woods. According to Aldous (1934) burning of bluestem grassland in Kansas did not decrease organic content or total nitrogen. Smith (1938) writes that experiments performed at the West Virginia Agricultural Experiment Station show that burning of broom sedge increases soil acidity. Deeply burned peat soils in Wisconsin showed a pH of 7.8 to 8.0 at the surface as compared with pH. 6.1 to 7.0 for most unburned peat except that supporting *Sphagnum* or *Chamaedaphne* which was 4.1 to 4.8 (Frolik). At the Illinois Agricultural Experiment Station plowing down cornstalks as compared with burning them and applying the ashes to the soil produced slightly higher yields. (Anonymous, 1938).

In eastern Nebraska experiments indicate that turning under 1 ton of straw per acre annually has cumulative beneficial effects. During the first 4 years of the experiment the average increase in yield of wheat on plots where wheat straw was turned under was one bushel per acre compared with plots where straw was not returned. During the second 4 years the increase was 3.3 bushels. For corn the increase in the first 4 years averaged 1.0 bushel and during the second 4 years 4.3 bushels. The authors conclude that returning straw to the land in eastern Nebraska is a soil-conserving practise, while burning the straw is soil-depleting (Weldon and Gross). Experiments in Indiana in turning under various residues (corn stalks averaging up to 3907 pounds per acre,

soybean straw 2777 pounds, wheat straw 1783 pounds) resulted in definite crop increases (Anonymous, 1938). Turning under wheat and barley straw in 4-year rotation tests at the North Dakota Agricultural Experiment Station in clay soil has had only slightly beneficial effects upon the crops (Stoa, 1938). At the Nephi Dry-farm Substation in Utah.

The average acre yield over the 14-year period from 1916 to 1929, inclusive, for burning all of the straw is 24.7 bushels, whereas the corresponding tillage treatment with all the straw plowed under gave an average acre yield of 23.4 bushels. Plots on which only the high stubble was burned yielded 25.2 bushels as compared with 24.5 bushels for the high stubble turned under. These differences, while not great enough to be significantly favorable to burning, are rather consistent over the entire 14-year period. While yearly burning of stubble is perhaps inadvisable, yet there may be reasons for burning once in several seasons, and these data indicate that no harmful effect is likely to follow, at least under present conditions" (Broken and Stewart, 1931).

Cole and Morgan (1938) call attention to observations at several experiment stations which indicate that soils in the Northern Great Plains blow more readily when they contain large amounts of decomposed organic matter and humus, as around old straw stacks and where alfalfa and sweet clover have been turned under.

5. FIRE AND PLANT SUCCESSION

Fire has for thousands of years been one of the chief initial causes of secondary plant succession. The voluminous amount of literature now available on this single subject has not been utilized as fully in land use and management as its importance justifies, but gradually ecological knowledge regarding plant succession is being recognized as part of the foundation upon which the superstructure of land planning must be built. The invasion and dense growth of many species, as the aspen, paper birch, lodgepole pine, fireweed, and bracken fern are so closely correlated to the burning of the previous vegetation as to characterize them as "burn indicators." These indicators possess one or more characteristics which enable them to become early invaders following fire, such as suitable devices for migration as wind-blown seeds or spores, rapid and dense growth, preservation of seed in the forest floor, opening of cones by fire, and capacity to produce root-sprouts (Clements, 1920). Following a severe burn in forests in western United States the first invaders are mostly mosses and liverworts, followed by annuals, and then by perennials. Shrubs, such as the raspberry and gooseberry, may come next or a grass stage may have preceded it. The shrubs are replaced by trees as aspen, alder, and birch; followed by other trees as the lodgepole pine, and then finally by the climax forest. The succession may begin with the aspen or even the lodgepole pine stage depending upon the severity of the fire. Stages in the secondary succession following fire in the northern hardwoods region as in southern New York are given by Wilm (1936) as (1) herbs and low shrubs, (2) raspberry-blackberry stage, (3) light demanding trees as aspen and pincherry, (4) mixed hardwoods as oaks, and (5) the climax, dominated by the beech and hard maple. These stages vary as to constituent species in different regions but the general pattern of succession following forest fire appears to

be similar to the two examples given. In grassland and shrub areas the later stages naturally do not appear.

Little is known regarding the time required for each stage in the succession. Huberman (1935) made a "rough approximation" that under conditions obtaining at Priest River in northern Idaho the time required to reach the climax would be 300 to 350 years, white pine would reach its peak in 120 to 180 years more, dropping out a period of 40 to 80 years additional, and the stabilization of the climax species, the hemlock, cedar and white fir, 40 to 60 years later; a total of 500 to 670 years. Reid, Isaac and Pickford (1938) have contributed much-needed definite data on succession in relation to time following fire in southwestern Washington.

Weeds, principally fireweed, formed approximately 50 percent of the total plant cover in 1925, 1 to 5 years after burning. In 1935, weeds were but a minor part of the vegetation, having been replaced by bracken on the double burn and the delayed burn and by shrubs (blackberry, vine maple, etc.) on the single burn. Reduction of weeds took place almost entirely between 1925 and 1927, the period of heaviest grazing.—Fire hazard was temporarily lowered by removal of the highly inflammable fireweed. On the double and delayed burns, the initial decrease in fire hazard was counteracted by the rapid and militant encroachment of bracken, which tends to become almost as inflammable as fireweed. On the single burn, substitution of shrubs for weeds has resulted in permanent reduction of fire hazard and considerably improved conditions for reforestation.—Grazing probably hastened the reduction in density of weeds, which are eaten readily by sheep, and thus favored increase in bracken or shrubs.—The data indicate that on cut-over Douglas fir lands similar to those used in this study and subjected to similar treatments the forage supply is ample during the 3 to 7 years following burning but dwindles thereafter, and that the potential duration of grazing on such lands is approximately 11 to 15 years.

Transeau (1935) has expressed relations of fire to forest and grasslands in the following succinct statement:

Fire favors the persistence of prairie species in contrast to tree species. Prairies preceded prairie fires. Whenever one searches the historical literature describing the period of settlement one is impressed by the frequent widespread fires usually ascribed to the Indians. Fire as an ecological factor, seems to boil down to this: that in forest climates it retards development, and may result in scrub, but it does not result in prairie. In a prairie climate it helps to maintain and perhaps rarely enlarges the prairie.

Land use of the coarser sand areas of the North Carolina Coastal Plain is dependent upon the "vicious circle" of coarse sand, dry vegetation composed chiefly of sandgrass, and fire. In an excellent paper Wells and Shunk (1931) have described the interrelations of these three in detail. The vegetation is made up chiefly of species that are capable of surviving frequent fires. Fire occurs so often and so certainly that succession is always stopped in the early stages. The chief reasons for this high frequency of fire is the heat of the white sands and the great inflammability of the very dry wire grass making the "sandhill country a huge tinderbox."

The retardation of succession or initiation of secondary succession by burning peat bogs and swamps has been described by several writers, especially Dachnowski-Stokes (1912, 1935). Adamson (1931) has called attention to the variety of climax communities on slopes of Table Mountain in South Africa due to recurrent fires.

It has been demonstrated that burning of sagebrush in various areas as in northern Colorado (Hanson, 1929) and in Utah (Stoddart, 1938) is followed by such great increases in the stand of grass as to indicate that the climax vegetation in these areas is grassland rather than sagebrush. Controlled grazing and prevention of repeated fires are necessary, following burning, or weedy grasses, as downy brome, and worthless shrubs, as little rabbitbrush and matchweed will invade (Pickford, 1932). On severely overgrazed and burned sagebrush areas, as well as on abandoned plowed lands, various weeds, as tansy mustard, tumble mustard, and flaxweed invade. These weeds serve as host plants during the spring to the beet leaf-hopper, the insect that transmits the curly top virus disease which causes such large periodic losses to sugar-beets, beans and tomatoes as to delimit the areas in which these crops can be successfully grown (Piemeisel and Chamberlin, 1936). Control of curly top disease is dependent upon plant succession replacing the early weed stage, in which mustards are prominent, by downy brome grass (requiring about 5 years in favorable locations), followed by perennial grasses and shrubs, and by prevention of overgrazing, excessive burning, unwise cultivation, and other practises which initiate the weed invasion.

As knowledge of plant succession and fire becomes more widely disseminated man will increasingly use them as tools in land management. For example, in southern California where chaparral fires frequently expose the soil to excessive runoff and erosion, succession has been speeded up by successfully sowing mustard by airplane (Weaver and Clements, 1938). Another example is furnished by Korstian (1937), who pointed out the need for encouraging succession by artificial planting on the burned and cut-over spruce lands of the southern Appalachians if coniferous cover is to be restored within a reasonable length of time. He stated that the best time for planting is immediately after a fire, provided adequate fire protection can be assured and where serious hardwood competition will not occur. Bews (1926) reports how the conflicting opinions regarding the value of burning grasslands in South Africa had developed and how they could be reconciled by analyses from the successional viewpoint of numerous observations. In moderately dry areas burning is injurious because it throws back the succession from the climax *Themeda* and *Andropogon* which are good grazing to an earlier stage dominated by relatively worthless species of *Aristida*, *Eragrostis* and others. In moister areas where forest is the climax burning tends to destroy Tambookie grasses and woody plants and causes the succession to revert to the earlier, desired *Themeda* and *Andropogon* stage.

Conclusion

Fire has been used as a tool in the following land management practises:

1. Destruction of debris as straw and other crop residues, logging slash, etc., to reduce fire hazard and to facilitate cropping or plant succession.
2. Destruction of pests such as weeds, insects and diseases.
3. Clearing land for cultivation or to improve conditions for desired plants

by burning trees and shrubs, weeds as Russian thistles, draining and burning bogs, and as a substitute for tillage in crop rotation.

4. Improving grazing conditions by destroying brush and trees, coarse grasses, dead vegetation, and to stimulate early spring growth.

5. Improving recreational areas.

In many of these practises fire as a tool has proven distinctly serviceable, in some cases it has caused irreparable damage, and in other cases it is doubtful whether the advantages were greater than the disadvantages, or not. It is the duty of research to determine fully and accurately the values and losses caused by fire not only to present existing vegetation, animal life, soils, etc., but also to the future conditions of the burned area. New uses or new disposal methods of residues and debris may be found. This duty can only be accomplished by painstaking measurements and observations involving various fields of science and lasting over a period of many years. At present the supply of scientific data of this sort is very meager. As such data accumulate fire as a tool in land use and management will be utilized far more efficiently by administrators than is possible at present.

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N. DAK. AGRIC. EXP. STATION,
FARGO, NORTH DAKOTA.

Preliminary Account of the New Albany Shale Flora

Charles B. Read and Guy Campbell

This paper is a preliminary statement bearing on the flora of the New Albany shale, its age, and its affinities. The list of plants shows that the flora is large for such an early one. It is interesting, therefore, both to the stratigrapher and to the botanist. On the one hand, it furnishes information regarding the age of the New Albany shale and in particular the upper portion of it, which has been discussed for many years; on the other hand, it supplies new data bearing on the morphological variations of these old plants.

The material which is the basis for this work was collected by the authors. The junior author, in particular, has made extensive collections in southern Indiana around New Albany, as well as in Kentucky.

This paper does not aim to present the purely stratigraphic problems or those arising from invertebrate evidence discussed at length in the more or less controversial papers dealing with the "black shales." These matters are treated in a manuscript by Campbell which will record the results of a very detailed study of the New Albany shale based on many years of work.

It is desirable however, to state briefly as a setting for the data here offered some of the elements of the general problem. Black shale intervals are conspicuous at about the same place in the section in the Appalachian province and in the regions flanking the Cincinnati arch, the Nashville dome, and the Ozark dome. Their ages and relationships have been and still are problems in the minds of most geologists. Some assign a lower Mississippian age to the shales, others regard them as Devonian, and still others regard them as in part Mississippian and in part Devonian. Some geologists are of the opinion that all these shales are of the same age, while some believe them to vary in age from place to place. The New Albany shale is one of these units; the Chattanooga and the Ohio are others; and in the Appalachian trough there are a number of these units, the nomenclature of which is complex, owing to lack of uniformity in names by various Surveys and to incomplete understanding of the relationships. The basis for the age determinations and correlations is in part paleontology and in part lithology. As stated above, no attempt is made to evaluate the evidence either of the relatively rare larger invertebrates, the abundant conodonts, or the occasional fish. Rather, this paper deals with the fossil plants, which constitute a line of evidence so far neglected.

In the systematic portion of the paper several species not previously described are discussed in a preliminary fashion. The complete flora is listed below to give a general idea of its composition.

Composition of the Flora

The composition of the flora is as follows:

EUTHALLOPHYTA

PHAEOPHYTA

- Prototaxites (Nematophyton) ortonii* Penhallow
Foerstia furcata (Dawson) Hirmer

CORMOPHYTA

PSILOPHYTA

ASTEROPHYTA

ASTEROXYLEAE

- Asteroxylon setchelli* n. sp.
Polyxylon elegans n. sp.

INCERTAE SEDIS

- Reimannia indianensis* n. sp.
Protolapidodendron microphyllum n. sp.
Mesoneuron simplex n. sp.

LYCOPSIDA

LEPIDOPHYTA

LEPIDODENDRACEAE

- Lepidodendron boylense* Read
Lepidodendron novalbanense n. sp.
Lepidodendron sp.
Lepidostrobus kentuckyensis Scott and Jeffrey
Lycopogonia callycyrtia Read

ARTICULATA

EQUISETALES

CALAMITACEAE

- Protocalamites dorfii* n. sp.

PTEROPSIDA

FILICINEAE

PRIMOFILICES

SIDARELLALES

- Sidarella scottii* Read

CLADOXLALES

- Pietzschia polyupsilon* n. sp.
Cladoxylon sp.
Steloxylon sanctae-crucis n. sp.
Steloxylon irvingense n. sp.
Steloxylon sp.
Hierogamma jeffreyi Read
Clepsydropsis campbelli Read
Clepsydropsis chaneyi n. sp.
Clepsydropsis bertrandi n. sp.
Clepsydropsis titan Read
Stereopteris annularis Scott and Jeffrey

INCERTAE SEDIS

- Microzygia lacunosa* Read

GYMNOSPERMAE

CYCADOFILICES

CALAMOPITYAE

- Calamopitys americana* Scott and Jeffrey
Calamopitys foerstei Read
Diichnia kentuckyensis Read
Kalymma lirata Read
Kalymma resinosa Read
Kalymma grandis Unger
Kalymma auriculata Read

Calamopteris hippocrepis Scott and Jeffrey
Stenomelon muratum Read

INCERTAE SEDIS

Periastron perforatum Scott and Jeffrey
Periastron reticulatum Unger
Lyginorachis dineuroides n. sp.
Plicorachis danvillensis n. sp.

CORDAITALES

PITYEAE

Archacopitys eastmanii Scott and Jeffrey
Callixylon brownii Read
Callixylon newberryi (Dawson) Elkins and Wieland
Arnoldella minuta Read

Representatives of the Psilophyta, Lepidophyta, Equisetales, Cladoxylales, Siderellales, Cydadoflicies, and Pityeae, i.e., most of the groups present and prevalent in the Carboniferous, are members of the flora. However, it contains in addition several clearly Devonian elements, such as *Asteroxylon setchelli*, *Polyxylon elegans* among the Psilophyta and *Pietzschia polyupsilon* among the Cladoxyleae. Such forms as *Protolpidodendron microphyllum* and *Reimania indianensis*, both of which are of doubtful affinities, are likewise definite Devonian types. And, considering the flora from an entirely different viewpoint, the general degree of advancement is that of a pre-Carboniferous flora. Doubtless the plants are specialized types, the specialization of which is in the nature of experimentation along different lines from that which characterizes the early Carboniferous. For example, *Siderella scotti* is a type which combines morphological characters known in the Carboniferous strata only in two distinct groups. *Protocalamites dorfii* is certainly more primitive than any other known calamitian species. Such genera as *Microzygia* and *Periastron* clearly show trends distinct from those of any Carboniferous plant.

Comparison with European Floras

Recent contributions by Bertrand,^{2,3} Böhm,^{2,4} Corsin,³ and Gothan⁶ relating to the flora of the Cypridinenschiefer at Saalfeld, Thuringia, the Wildenfels beds in Saxony, and the lydites of the Montagne Noire in southern France are of great importance. These floras are of more than usual interest to American students of the Carboniferous and Devonian since they not only clarify certain aspects of these early floras but also are of interest in connection with the determination of the age of certain beds in America. It seems desirable to summarize these papers briefly, stressing particularly those portions which relate to American problems.

The most important of these papers is Paul Bertrand's "Contribution à l'étude des Cladoxylées de Saalfeld,"³ which deals primarily with the Cladoxylons collected in the Saalfeld area in Thuringia and is the result of studies extending over two decades. Bertrand concludes that these enigmatic plants are Filicales belonging in a separate family, the Cladoxyleae, and closely related to the Zygopterideae. The details of morphology of these plants are ably discussed, and 12 nominal species are recognized. These are *Cladoxylon*

taeniatum Unger, *Cladoxylon mirabile* Unger, *C. solmsi* P. Bertrand, *C. radiatum* Unger, *Hierogamma mysticum* Unger, *H. calopicum* P. Bertrand, *Syncardia pusilla* Unger, *Arctopodum insigne* Unger, *Clepsydropsis excelsa* P. Bertrand, *Clepsydropsis elongata* P. Bertrand, *Clepsydropsis exigua* P. Bertrand, and *C. antiqua* Unger (pars). It is impossible to summarize the wealth of information concerning this group. The genera listed fall into the category of organ genera. Thus *Cladoxylon* includes stems with radial symmetry, *Hierogamma* and *Syncardia* include branches with dorsiventral structure, and *Clepsydropsis* includes aphanleptoid ramifications and phyllophores. It is further suggested that *Steloxylon* species are rootlike structures pertaining to the group. Consequently, the species (in the ordinary meaning of the word) are but 6.

The complete flora as listed by Bertrand includes:

Lepidodendron richteri Unger, *L. saalfeldense* Solms, *L. nothum* Unger, *Archaeocalamites scrobiculatus* Schlotheim, *Sphenophyllum insigne* Williamson, *Metaclepsydropsis paradoxa* Unger, *Metaclepsydropsis* spp., *Calamopitys saturni* Unger, *C. annularis* Unger, *Kalymma grandis* Unger, *Megalorachis elliptica* Unger, *Sparganium anemoides* Unger, *Calamopteris debetis* Unger, *Stephanida gracilis* Unger, *Araucaroxylen* Unger, *Aporoxylen primigenium* Unger, and *Periostron reticulatum* Unger.

The plants occur in the *Cypridina* shales and were discovered by Richter, who recorded them in 1856. The shales carry a marine fauna which Richter regarded as Devonian. It is important to note, however, that this Devonian fauna occurs in horizons below the plant-bearing strata. The latter are for the most part, gray shales containing phosphatic nodules carrying the petrifications.

Of great importance in determining the age of the Saalfeld occurrence is the presence of similar plant remains in the "horizon à lydiennes" at the base of the Carboniferous in the Montagne Noire on the southern edge of the central plateau of France. This flora has recently been summarized by Böhm¹ and by Bertrand, Böhm, and Corsin.² It contains *Lepidostrobus browni* (Unger) Schimper, cf. *Sphenophyllum* sp., *Cladoxylon taeniatum*, Unger, *Cladoxylon* sp. cf. *C. taeniatum*, *Cladoxylon* n. sp., cf. *Metaclepsydropsis* sp., *Calamopitys blayaci* Corsin, *Periastron delepinei* Corsin, cf. *Cyclopteris* sp.

At the same horizon are found the goniatites *Aganides ornatissimus* de Koninck, *Pericyclus kochi* Holzapfel, *P. hauchecornei* Holzapfel, *P. fasciculatus* McCoy, *P. niger* Delépine, *Nomismoceras frechi* Schmidt, and *Prolecanites* sp. Of this fauna, the second, third, and sixth forms listed are known only from the lower Viséan.

It is apparent that the flora of the lydite horizon has a striking affinity with that of the *Cypridina* shales at Saalfeld. This is brought out particularly by the *Cladoxylons* and suggested by the related *Calamopitys* and *Periastrons*.

Bertrand, Böhm, Delépine, and Corsin² believe that the Saalfeld flora and the lydite flora are Viséan in age. This conclusion is based partly on the associated fauna, but also to a considerable extent upon a statement in the

literature that a very similar flora occurs in Kentucky at the base of the †Waverly (New Providence) shale.¹⁰ In 1933 one of the writers (Read) orally corroborated this, basing his opinion on the purely local sequence of strata. At that time it was difficult to understand why such early plant types were present in Osage (Mississippian) strata, but the stratigraphic evidence seemed irrefutable. Since then, field studies carried on primarily by Campbell prove that the Kentucky floras are from strata which are correlative with beds of New Albany age in Indiana. Full information concerning this is presented in a paper by Campbell now in manuscript form. The important point is that the flora occurs in rocks which are of New Albany age and not of New Providence age. In other words, the Kentucky occurrence of the *Calamopitys* flora cannot be cited as proof of the Osage age of the European floras.

Gothan, on the other hand, suggested that the Saalfeld flora is Upper Devonian, on the basis of the occurrence of *Pietzschia schilleri* Gothan in the "gisement de Weldenfels" in Saxony.⁶ This form, obviously related to *Cladoxylon* and preserved similarly to the Saalfeld material, is found in beds held to be Upper Devonian. No attempt is made in this paper to date the European floras just discussed. However, as they are referred by several authorities to the lower Viséan, some of the evidence upon which this determination of age is based is reviewed.

The flora referred to above and believed by Bertrand to be strong evidence favoring the Viséan age of the Saalfeld flora is the Junction City, Kentucky, flora reported from the †Waverly shale by Scott and Jeffrey¹⁰ in 1914. At that time, 6 forms, *Calamopitys americana* Scott and Jeffrey, *Calamopteris hippocrepis* Scott and Jeffrey, *Periastron perforatum* Scott and Jeffrey, *Archaeopitys eastmanii* Scott and Jeffrey, *Steropteris annularis* Scott and Jeffrey, and *Lepidostrobus kentuckiensis* Scott and Jeffrey, were described.

To this flora may be added numerous forms including new calamopityean types, *Periastron reticulatum* Unger, *Stenomyelon muratum*, *Pietzschia polyupsilon*, new lycopodiaceous forms, and several new fern types. The complete list of plants from the New Albany is given elsewhere in the paper.

The New Albany flora, including the Junction City flora, is similar to but distinctly older than either of the European floras discussed. In the families Calamopityeae, Lepidodendraceae, and to some extent in the Cladoxyleae, as well is in the species of *Periastron*, there are elements of strong similarity, if not identity. The occurrence of *Sphenophyllum insigne* and of *Melaclepsydropsis duplex* in the Saalfeld flora hints at a younger age than that indicated by anything yet seen in the New Albany. The Psilophytales, *Protocalamites*, *Siderella*, *Reimannia*, *Callixylon*, and *Pietzschia*, all point to an earlier age than that of either the Saalfeld or the lydite flora. There are no records of lower Carboniferous or of Mississippian Psilophytales. This group, as well as several isolated genera which occur in the New Albany, is primitive and is generally accepted as Devonian. The same applies to species of *Callixylon*. It is well-known in the Devonian. It is also common in the New Albany,

and, while there are reports of this genus in Mississippian beds, all of these are doubtful. In short, this upper New Albany flora is distinctly Upper Devonian.

Bertrand regards the floras of Saalfeld, St. Nazaire, and of Kentucky (New Albany) as the earliest traces of the coal floras of higher Carboniferous strata.³ To a certain extent this is true. However, it is doubtful if this flora is more suggestive of the succession of Coal Measures floras than is the assemblage of plants characteristic of the other Upper Devonian terrains, and affinity with the later floras does not necessarily imply Carboniferous age for the New Albany floras.

There can be no doubt that the New Albany and its correlatives include beds which lie close to the Devonian-Carboniferous boundary. The lack of agreement of the evidence definitely indicates this. The base of the New Albany is certainly Devonian and possibly as old as the Tully. The uppermost beds are, according to some observers, also Upper Devonian but according to others, oldest Kinderhook. The plants suggest a Devonian age, and it is, indeed, undesirable to indicate a systematic boundary within a series so uniform and so completely lacking in any recognizable break of any consequence. The senior author recommends, with the consent of the junior author, that the Devonian-Mississippian line be drawn at least above the uppermost plant bed in the New Albany.

CONCLUSIONS REGARDING THE AGE OF THE FLORA

In the preceding discussion it has been shown that flora of the New Albany shale is characterized by:

1. The occurrence of the Psilophyta, Lepidophyta, Equisetales, Cladoxy-lales, Sidarellales, Cycadofilices, and Pityeae.

Thus there are present most of the groups common in the lower Carboniferous. The Psilophyta, as well as some other groups less well understood, are, however, important Devonian elements which cannot be disregarded.

2. The presence of forms showing signs of earlier specialization than those in the Carboniferous.

The most nearly comparable floras, e.g., that from the *Cypridina* shales and that in the vicinity of St. Nazaire in the Montagne Noire in Germany and southern France, are dated on insufficient evidence. The occurrence of goniatites suggesting to some extent a Visean age and the comparison with the New Albany flora, which at one time was believed to occur in strata of Osage age, have been the chief arguments cited by Europeans for regarding these floras as Carboniferous. It is now clear that the latter argument can be no longer upheld. Perhaps the evidence of the former should be reconsidered. At any rate, the flora of the upper part of the New Albany can be regarded only as Upper Devonian.

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Descriptions of Species

Prototaxites ortonii Penhallow⁸

Plate 5, Fig. 3

1. General structure open, consisting of a loose network of broad, tubular cells and occasional small areas of small hyphae tightly bound together, the so-called medullary spots.

2. Transverse section marked by a relatively large number of the large cells cut in transverse section as contrasted with the radial and tangential sections where the majority of the cells are cut longitudinally.

3. Medullary spots small, circular in section, consisting of a dense mass of very small, tightly interwoven hyphae.

4. Large cells embedded in an open network of small hyphae which are poorly preserved in the material at hand.

Foerstia furcata (Dawson) Hirmer⁷

Plate 4, Fig. 1

This species, originally described by Dawson as *Sporocarpion furcatum*, was later described by White as *Foerstia ohioensis*.¹³ The nomenclatorial difficulty has been adjusted more recently by Hirmer.

The detailed accounts of this species by White and by Lang make a description unnecessary. The material has been compared with *Fucus* and is referred to the brown algae.

Asteroxylon setchelli sp. nov.

Plate 4, Fig. 2

1. Stems small, the specimens seen less than 5 mm. in diameter.

2. Stele stellate, consisting of five radiating arms centrally united to form a relatively stocky solid cylinder.

3. Phloem and outer stelar tissues problematical but probably concentric.

4. Protolylem exarch to slightly immersed.

5. Outer tissues parenchymatous as observed, with some traces of a thick-walled hypodermis.

Polyxylon elegans sp. nov.

Plate 2, Figs. 1 and 5

1. Stem small, 5 to 8 mm. in diameter.

2. Bundles several, in the specimens observed 4; shape that of an open U with forked apices; bundles amphicribal.

3. Xylem of large tracheids, scalariform.

4. Phloem problematical, apparently surrounding the xylem and conforming to the contours of the xylem, narrow, 2 to 3 cells, limited by a questionable endodermis.

5. Groundmass parenchymatous, no outer tissues seen.

6. Lateral appendage absent or not preserved.

Reimannia indianensis sp. nov.

Plate 4, Fig. 5

1. Stem small, 2 to 3 cm. in diameter in the specimen seen.
2. Stele small, centrally located, T shaped. amphicribal.
3. Xylem mesarch, forming well-defined loops near the apices of the arms.
4. Outer stelar tissues poorly preserved.
5. Cortex parenchymatous, with outer tissues inclined to be sclerenchymatous.
6. Appendages unobserved.

Protolapidodendron microphyllum sp. nov.

Plate 3, Figs. 1 and 2

1. Stem small, about 8 mm. in diameter.
2. Stele trilobed, the three lobes united to form a narrow central column.
3. Xylem mesarch, the protoxylem situated near the apices of the arms and forming loops.
4. Outer stelar tissues not preserved.
5. Cortex parenchymatous and limited by a sclerotic hypodermis.
6. Leaves scalelike both in aspect and in origin, parenchymatous.
7. The leaves bifurcating a short distance above the point of attachment, exact outline unknown, but probably linear.

Mesoneuron simplex sp. nov.

Plate 5, Fig. 1

1. Stem small, 2 to 3 mm. in diameter, carrying a small protostele.
2. Protostele irregularly lobate, tending to be T-shaped, protoxylem points several, mesarch.
3. Adjacent phloem(?) following the contour of the xylem, very limited in extent.
4. Cortex consisting of an inner parenchymatous zone and a thin outer sclerotic hypodermis.

This form is clearly related to *Mesoneuron tripos* of Unger. Its affinities are for the present highly problematical.

Lepidodendron boylense Read⁹

Lepidodendron boylense is the common lepidodendroid species occurring in the New Albany of southern Indiana. Well-preserved steles, as well as portions of the characteristic cortex, are fairly numerous.

Lepidodendron novalbaniense sp. nov.

Plate 5, Figs. 2 and 4

1. Stems small.
2. Stele of the solid or protostelic type with a slight admixture of parenchyma, protoxylem exarch, at the points on the scalloped edge of the xylem.
3. Secondary xylem forming a narrow zone.

4. Outer stelar tissues not well preserved.

5. Cortex parenchymatous, large celled, containing numerous leaf traces which are small, circular, mesarch-concentric in structure. Leaf traces derived from the points of the xylem and pass out abundantly through the secondary xylem, there forming large raylike structures.

Lepidodendron sp.

The material included under this heading consists of fragments of the outer and middle cortex of a small stem of *Lepidodendron*, or some allied form. The cortical tissue is apparently parenchymatous but moderately thick-walled, and carries embedded in it numerous vascular bundles, which are very poorly preserved but which appear to have a mesarch structure and which occupy the outer portion of large, open areas almost entirely devoid of cellular structure and evidently originally marked by delicate parenchyma. While the specimens are, in some cases, complete but crushed cylinders, the inner tissues including the cauline stele are missing. In consequence, the fossil is here listed simply as *Lepidodendron* sp.

Protocalamites dorfi sp. nov.

Plate 4, Figs. 3 and 4

1. Stem small to medium in size according to the fragments in hand, rather woody, pith large, secondary wood zone wide.

2. Primary xylem forming large bundles in contact with the secondary growth, these more or less circular in transverse section, mesarch tending toward endarch, canals absent, protoxylems forming large prominent areas.

3. Rays broad but poorly defined, similar to elements of secondary xylem.

4. Leaf traces small, fan shaped, endarch mesarch.

5. Vascular bundles alternate at the nodes.

Siderella scotti Read⁶

Remains of this species, first recognized from collections made at Junction City, Kentucky, have been observed at several localities in the New Albany shale of the New Albany district, southern Indiana. In general, the species is represented there by small fragments which do not present the details of structure described in the original material.

PIETZSCHIA Gothan⁶

Pietzschia polyupsilon n. sp.

Plate 2, Figs. 2 and 6

1. Stem of medium size (25 mm. \pm), circular, radially symmetrical, and consisting of a ring of radially aligned vascular bundles, an inner parenchymatous groundmass, and an outer sclerotic and parenchymatous cortex.

2. The vascular bundles of the ring ranging from .25 to .35 mm. across, the number of bundles high, about 54 in the type specimen.

3. Vascular strands concentric in general structure, with a centrally situated and elongate xylem, consisting entirely of primary wood in which several

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protoxylem groups are situated, and the whole surrounded by a delicately-walled parenchymatous tissue, unquestionably the phloem.

4. The central groundmass predominantly parenchyma but carrying scattered sclerenchyma strands which become more numerous outward and not infrequently form plates between the vascular bundles.

5. The cortex likewise a parenchymatous mass with frequent sclerenchyma strands and carrying the traces to lateral organs described below.

The vascular bundles frequently branched and anastomosing, forming strands Y-shaped as well as bar-shaped in cross-section. Occasional circum-medullary bundles likewise develop. These are circular and small.

7. In the development of the trace to the lateral organs four bundles are involved. From the peripheral portion of each a bundle is pinched off, these being concentric. As these pass outward and upward they form two \sqcap -shaped bundles as a result of pairing and fusing, with resultant elongation and with some multiplication of protoxylems. No later stages have been observed.

This genus has been previously known only from the Wildenfels shale, Saxony, whence the type species was described by Gothan. As was then indicated, *Pietzschia* is clearly related to *Cladoxylon* but differs in the reduction of the "boucle" or loop and in the absence of any tendency toward secondary xylem development. The arrangement of the vascular strands into a well-defined ring surrounding the central undifferentiated "medulla" is likewise a point of distinction from the known species of *Cladoxylon*.

The lateral organs here described are of the type regarded by Bertrand as dorsiventral branches and not infrequently bearing phyllophores. The behavior of these bundles suggests leaf traces, particularly in their apparent dorsiventral orientation. No specimen of a phyllophore has been seen which on histological grounds can be related to this stem.

STELOXYLON Solms¹¹

Steloxylon irvingense sp. nov.

Plate 1, Figs. 1 and 3

1. Stem rather large, in the type specimen 60 by 30 mm. in diameter, consisting of a predominantly parenchymatous groundmass in which are embedded small, anastomosing vascular bundles.

2. Groundmass consisting, as previously indicated, of parenchyma, in which are embedded irregular strands of very thick-walled, small-lumened sclerenchyma (stone cells).

3. Vascular bundles small, ranging in diameter from 0.8 to 1.7 cm., concentric in structure. Xylem occupying the central portion, primary xylem large, 3 to 7 mm. in diameter; protoxylem slightly eccentric usually. Secondary xylem unequally developed, more abundant on one side than on the other, frequently lacking on a short arc, usually only a few elements (1 to 7) in thickness. Outer stellar tissues not preserved.

4. Vascular bundles numerous, dichotomizing and apparently anastomosing.

The reference of this specimen to *Steloxylon* follows a modification of the generic definition insofar as the occurrence of primary xylem is concerned. The presence of the sclerotic masses in the parenchymatous groundmass provides a recognizable specific distinction.

***Steloxylon sanctae-crucis* sp. nov.**

Plate 1, Figs. 2, 4, and 5

This species is similar to *Steloxylon irvingense* in general features but differs as follows:

1. The vascular bundles large, from 6 to 38 mm. in diameter, secondary xylem forming a considerable mass, up to 10 tracheids in thickness.
2. The groundmass parenchymatous, without bundles of sclerenchyma.

Steloxylon sp.

Under this heading is included a single very fragmentary specimen of a *Steloxylon*-like plant with small, scattered bundles of concentric, vascular tissue consisting almost entirely of primary xylem and with only the beginning of secondary growth. Embedded in the parenchymatous groundmass are small strands of sclerenchyma. The structure is very similar to that of *Stenomyelon irvingense* yet differs in the almost complete absence of secondary growth. It is with some hesitation that the writer places this form under a separate heading, but it is probably best to do so temporarily.

***Clepsydropsis bertrandi* sp. nov.**

Plate 3, Fig. 4

1. Phyllophore small, about 6 mm. in diameter.
2. Vascular bundle small, cross-section about 1 mm. long and $\frac{1}{2}$ mm. wide, dumbbell-shaped with a slight medial constriction and slightly swollen ends, surrounded by a narrow zone of disorganized tissue probably referable to the phloem.
3. Groundmass of the phyllophore rather large-celled, parenchyma becoming progressively smaller-lumened towards the exterior, where the outer 10 or 12 layers of cells show considerable evidence of secondary thickening of the walls.
4. Loops small, carrying the remains of protoxylem and partly disorganized parenchyma.
5. Lateral traces concentric but tending to be c-shaped, small, originating from the ends of the vascular strand by a division of the tissues in the loop, followed by slow constriction and separation of adjacent xylem from the main strand.
6. Pinna trace markedly decurrent on the phyllophore as indicated by the deep groove marking its position on the exterior of the structure.

***Clepsydropsis chaneyi* sp. nov.**

Plate 2, Fig. 4

1. Phyllophores small, 5 to 6 mm. in diameter.
2. Vascular bundle small, oval in transverse section, broadest in central

area, surrounded by a narrow zone of disorganized tissue of apparently parenchymatous nature and referable to phloem.

3. Outer tissues (groundmass) parenchymatous and similar to *Clepsydropsis bertrandi*.

4. Loops large, parenchymatous.

5. Vascular traces to pinnae unknown.

Kalymma lirata Read⁹

The details of the morphology of this petiole have already been recorded in two papers. This species is present, although rare, in the uppermost New Albany shale in southern Indiana but is quite common in the nodular upper New Albany in Kentucky at all points where that horizon is sufficiently well exposed for collecting.

Periastron perforatum Scott and Jeffrey¹⁰

This species, likewise well known, has been observed at numerous localities in southern Indiana. In fact it is one of the most common forms present but usually occurs in fragmentary state.

Lyginorachis dineuroides sp. nov.

Plate 2, Fig. 3

1. Rachis small, oval, carrying two vascular bundles.
2. Vascular bundles flattened, cross-sections with irregularly swollen ends; protoxylem exarch, outer stelar tissues concentric around the xylem.
3. Groundmass of tissue large angular parenchyma.
4. Outer portion of petiole a sclerenchymatous hypodermis.

Plicorachis danvillensis sp. nov.

Plate 3, Fig. 3

1. Petiole small, about 7 by 10 mm. in oval cross-section, outer tissues in the type specimen not preserved.
2. Groundmass of the petiole parenchymatous.
3. Vascular system consisting of a single dorsiventral, plicated bundle with numerous mesarch protoxylems.
4. Protoxylems situated at both the points of the plications and in the bases of the folds.

Callixylon newberryi (Dawson) Arnold¹

The records of abundant material of *Callixylon newberryi*, or "*Dadoxylon*" as it was formerly named, have long been in the literature. Specimens of this species make up most, if not all, of the large silicified remains which occur chiefly in the upper half of the New Albany, near the top but below the main plant zone.

Callixylon browni Read⁹

Callixylon browni has been noted from the upper part of the New Albany of southern Indiana and also at Holy Cross, Ky., although at both points

only individual specimens are in the collections. It seems to be fairly characteristic of the upper horizon.

Arnoldella minuta Read¹⁹

Arnoldella minuta was described by the writer from a few small specimens from Junction City, Kentucky. Since then several additional specimens have been found and examined from Junction City and from other localities, including some north of the Ohio River in the New Albany district all of which corroborate the original diagnosis. Originally suggested to be petioles of some member of the Pityeae this fossil appears now to represent some member of the Cycadofilices, although the writers found it impossible to relate it to any known form.

Protosalvinia ravenna White¹³

White has placed the sporangia which occur so abundantly in the New Albany shales at many localities in this species, but their exact affinities, however, remain doubtful. He referred them tentatively to the Lepidodendraceae on the basis of certain morphological features.

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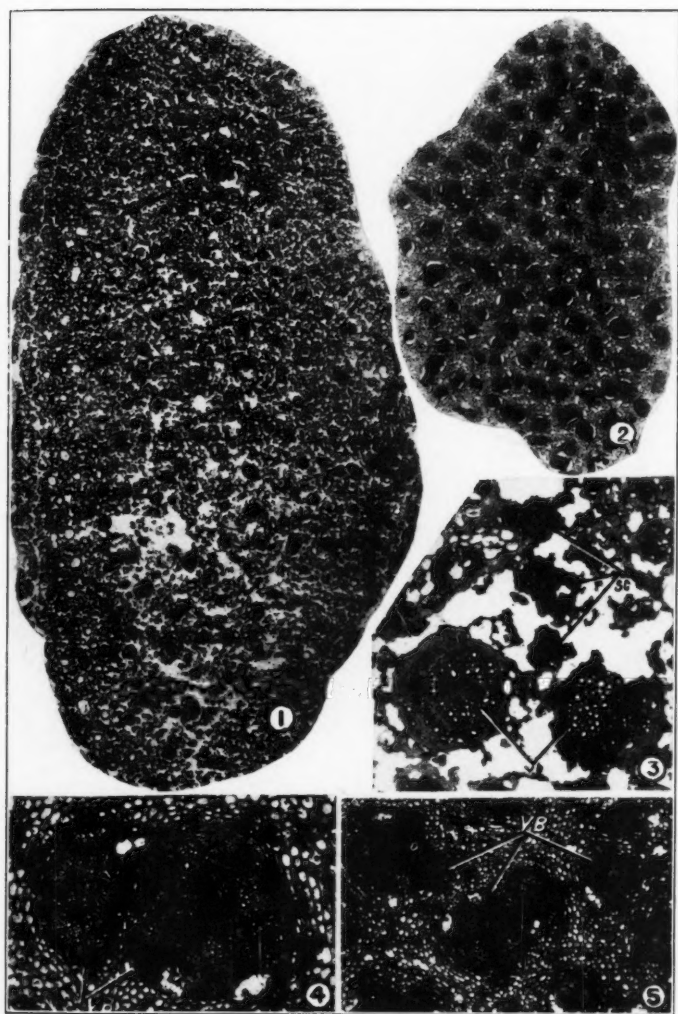


PLATE 1—(x1-1/3), 3 (x20). Photographs of *Steloxylon irvingense* illustrating the general aspect of the stem and the numerous vascular bundles (Fig. 1) and the details of two vascular bundles (vb) and the adjacent cortical tissue (Fig. 3). Note the sclerotic strands at sc.; Figs. 2 (x1-1/3), 4 (x17), 5 (x7). Photographs of *Steloxylon sanctae crucis* showing the numerous vascular bundles scattered through the stem (Fig. 2) and the details of the vascular bundles (vb) (Figs. 4, 5). Note the absence of the sclerotic strands which are characteristic of the cortex of *S. irvingense*.

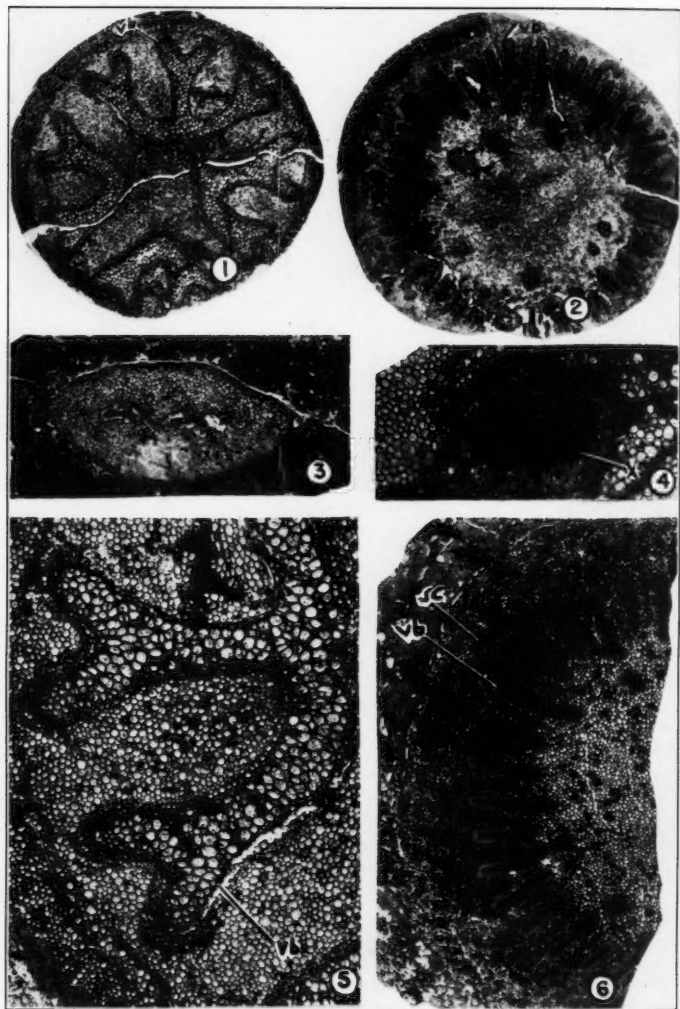


PLATE 2—Figs. 1 (x5), 5 (x20). Photographs of *Polyxylon elegans* showing the aspect of the stem (Fig. 1) and the details of the vascular bundle (vb). (Fig. 5); Figs. 2 (x2), 6 (x5). Photographs of *Pietzschia polyupsilon* showing the general features of the stem (Fig. 2) and a somewhat more detailed view of another specimen showing the structure of the vascular bundles (vb) and the numerous sclerotic strands in the cortex; Fig. 3 (x5). Photograph of *Lyginorachis dineuroides* showing the position of the vascular bundles; Fig. 4 (x17). *Clepsydropsis chaneysii* showing the form of the vascular bundle and the large peripheral loops.

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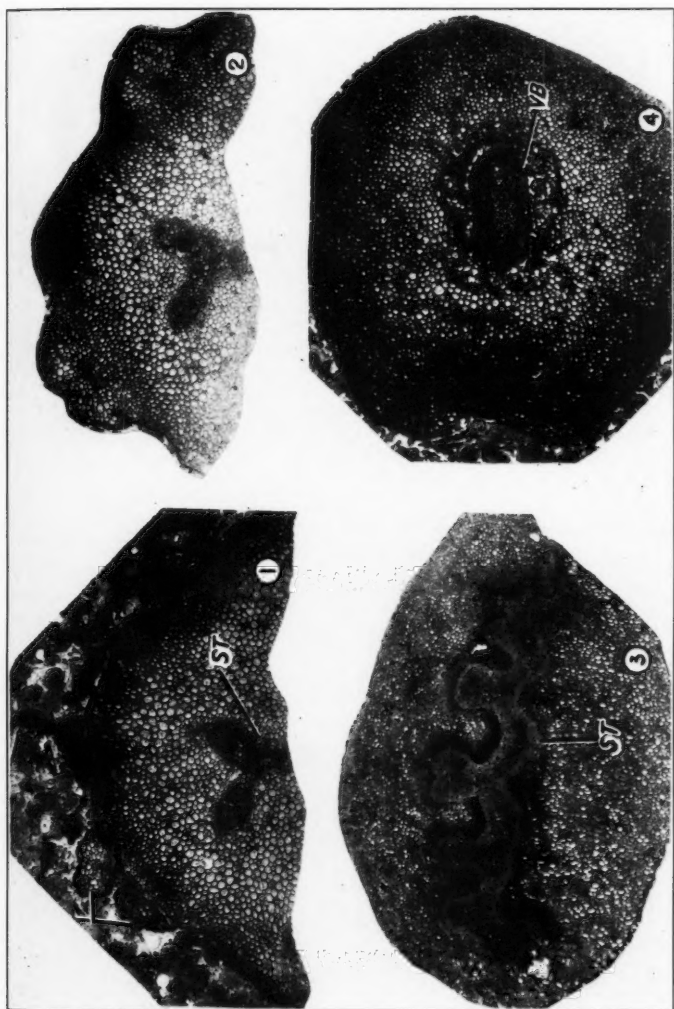


PLATE 3—Figs. 1 (x17), 2 (x17). Photographs of *Protolpidodendron microphyllum* showing the triangular or Y-shaped stele (st) and the scale leaves (l) which appears to be without vascular supply; Fig. 3 (x25). *Plicorachis danvillensis* showing the convoluted stele (st); Fig. 4 (x17). *Clepsydropsis bertrandi* showing the general aspect of the phyllophore and the vascular bundle (vb).

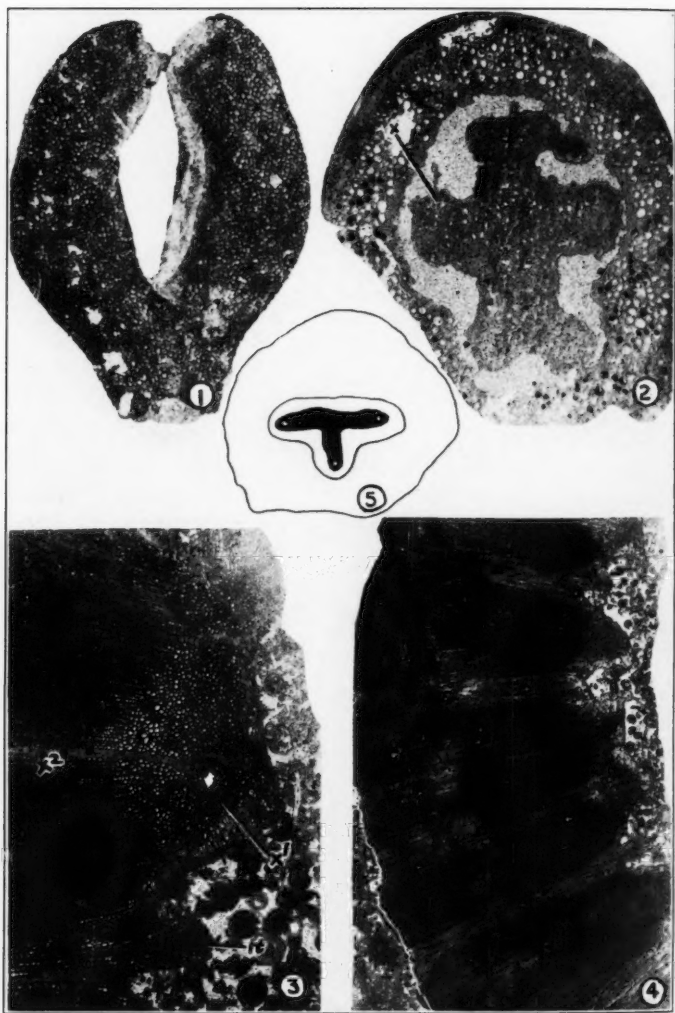


PLATE 4—Fig. 1 (x20). Photograph of *Foerstia furcata* showing the form of the thallus-like body; Fig. 2 (x20). *Asteroxylon setchelli* showing the irregularly lobate stele and the cortex. The clear space adjacent to the xylem (x) was apparently occupied by the phloem; Figs. 3 (x13), 4 (x5). Photographs of *Protocalamites dorfi* showing the solid primary xylem (x¹), the leaf trace (lt), and the secondary wood (x²); Fig. 5 (x20) Camera lucida sketch of *Reimannia indianensis* n.sp. showing the outline of the stele.

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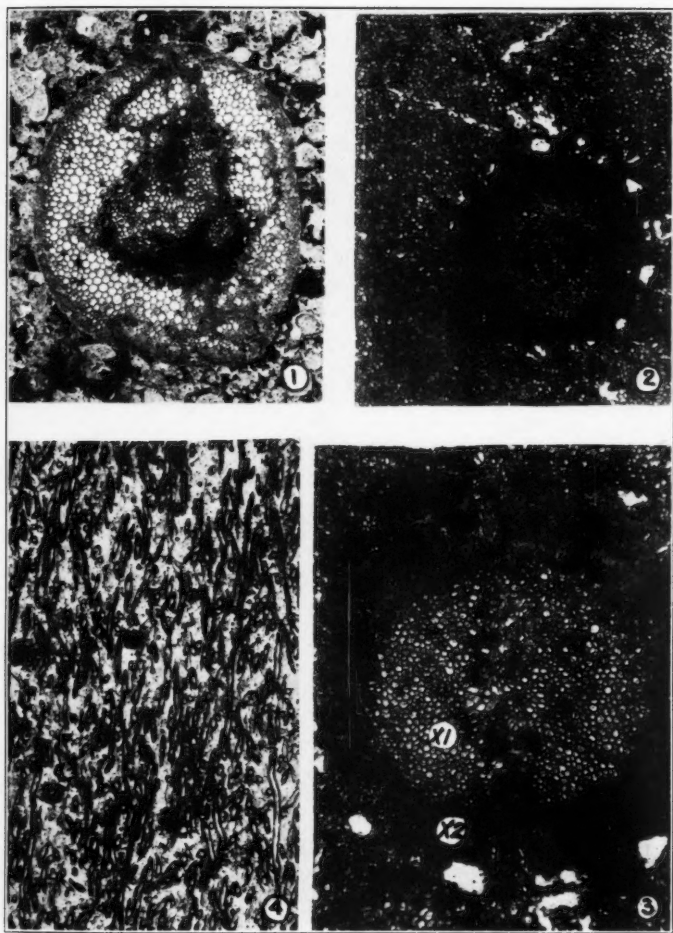


PLATE 5—Fig. 1 (x20). *Mesoneuron simplex* showing the general features of the stem; Figs. 2 (x7), 4 (x17). *Lepidodendron novalbaniense* showing the general features and the details of stelar structure (x1, primary xylem; x2, secondary xylem); Fig. 3 (x17). *Prototaxites* (*Nematophyton*) *ortoni* showing the general features as seen in longitudinal section.

Notes on the Fossil Flora of Yellowstone National Park with Particular Reference to the Gallatin Region

H. N. Andrews

Previous to the study of the coniferous woods of the Lamar River Flora by Read (1933) the extinct plants of Yellowstone Park had received very little attention since the appearance of Knowlton's monograph in 1899. This is rather surprising in view of the fact that it is a region where well-preserved wood and leaf impressions exist in close association but it is probably attributable to the general lack of scientific interest in fossilized woods, and to the fact that Knowlton's treatment of the leaf impressions was a reasonably complete and carefully executed study.

Investigations have been largely confined to the famous Specimen Ridge and Fossil Forest localities which lie immediately north of the Lamar River. The greater part of Knowlton's specimens came from this locality and Read's material which forms the basis of his recent revision of the coniferous woods of the Lamar River Flora is likewise from the same region. The fossil forests of the Yellowstone, however, are by no means confined to the Lamar River Valley, for in the northwest corner of the Park lies another Fossil Forest¹ fully as spectacular as regards the size and abundance of the fossilized stumps and logs as in the better known area.

In the summer of 1936 a representative collection of fossil wood was made at this place which lies immediately north of the lower reaches of Specimen Creek in the northwest corner of the Park. This locality, separated as it is from the better known fossil plant region in the northern and northeast part of the Park by some 50 miles, has recently been described in an interesting popular paper by the Chapmans (1935). But the fossil stumps and logs found so abundantly there have not to my knowledge received histological study. From personal observations it seems quite clear that the Fossil Forests of the Park and nearby regions are more extensive than was suspected by the earlier workers. In his monograph (based on plants collected primarily from the Lamar River Valley) Knowlton (1899) notes that:

Fossil trees or fragments of wood of greater or less size are found in many parts of the Park, but their distribution is mainly confined to the north and northeastern portions. The forests of standing trees are all found in the vicinity of the Lamar River, the most striking being exposed on the slopes and cliffs of Amethyst Mountain and Specimen Ridge.

¹ On the United States Geological Survey Topographic Map of the Yellowstone National Park there will be found two Fossil Forests—one shortly southeast of Specimen Ridge in the Lamar River Valley and the second in the northwest corner of the Park near the Gallatin Ranger Station. It is to the latter Forest that the reference applies.

In 1896 Knowlton described a fossil pine wood (*Pityoxylon Pealei*) from the Upper Gallatin Basin, Montana, and commented on the general similarity of the beds there to those of the Fossil Forest in the Lamar River region within the Park. The wood he describes was probably collected near the locality where our own studies have been made and quite likely from a part of the same formation.

Our collections were taken from the bed of the branch of Specimen Creek immediately east of the Gallatin Fossil Forest whose location is shown on the previously mentioned topographic map. The bed of the Creek which drains the nearby ravine shown in Fig. 2 is littered with fossilized wood which had weathered from the upper parts of the surrounding hills. A portion of the latter appears at closer range in Fig. 7. It is in these beds of ash and breccia that the erect stumps and logs occur in such abundance. Specimens were also collected from the southwest and southern slopes of Big Horn Peak where at least 12 successive fossil forests were counted in the strata and where, indeed, careful studies might add to the number. The general appearance of the fossil-bearing formation is much the same here as in the Lamar River region and both are probably of Eocene (Field, 1932) age.

The southern slopes of Big Horn Peak are likewise littered with fragments of fossil wood. Four stumps with individual measurements of at least 8 feet in diameter were observed. Unfortunately their woods were found consistently to be too highly silicified to warrant sectioning, but from macroscopic observations it may reasonably be assumed that they are of sequoian affinities. An attempt was made to determine the age of one of these giants. The wood was lacking from the central portion, the resulting cavity being filled by a core of volcanic breccia three feet in diameter. The average number of rings per inch in the portion of the stump remaining proved to be 18, which indicates an age exceeding 860 years. Taking into account the fact that in the central missing core there would be somewhat fewer rings per inch and that considerable wood had apparently been lost from the outside, 800 years seems a conservative estimate of the age of this particular tree.

As has been well shown by the Chapmans (1935), the abundance and spectacular size of many of the erect and prostrate trunks is fully equal to those to be found in the better known deposits of the Specimen Ridge and Fossil regions of the Lamar River Valley.

From our collections we have identified several woods² by their histological features. We may first consider:

Sequoia magnifica Knowlton

Sequoia magnifica was apparently abundant in this region of the Park. Sections of a well-preserved fragment collected on the west flank of Big Horn Peak and likewise from two others collected from Specimen Creek have been

² The living flora of this region of the Park as in most other portions is dominantly coniferous. The following species growing on the site of the Eocene forests are of common occurrence: *Pseudotsuga taxifolia*, *Picea Engelmanii*, *Abies lasiocarpa*, and *Pinus albicaulis*.

prepared. A few variations from the published descriptions of this species founded upon specimens gathered from the Lamar Valley (Knowlton, 1899; Read, 1933) have been noted in our specimens. The rays frequently reach a height of 45 cells, and triseriate pitting on the radial walls of the tracheids has been observed. These differences lie within the bounds of expected variation and from comparisons with specimens of *S. magnifica* from Elk Creek³ there seems little doubt that this is the same species reported by previous writers from the Lamar Valley.

Fragmentary impressions of foliage were also discovered in the locality on Big Horn Creek which compare closely with that of the living *Sequoia sempervirens*. This foliage (Fig. 6) likewise shows a similarity to the impressions known as *Sequoia Langsdorfii* (Brgnt.) Heer described by Knowlton (1899), a species which has been collected from many localities in the northern and northeastern part of the Park. According to Knowlton *Sequoia Langsdorfii*:

—is by far the most abundant and widely distributed conifer found in the Yellowstone National Park, with the possible exception of *Sequoia magnifica*, known only from internal structure. It occurs in many places and in a variety of forms—that is to say, the branchlets and leaves are of various sizes, showing that they have come from many individuals and from different parts of the tree.

In consideration of the abundance of this foliage as reported by Knowlton from the vicinity of the Lamar River Valley and its presence in the northwest corner of the Park as shown here, together with the wide distribution and abundance of the wood of *Sequoia magnifica* the conclusion lies close at hand that these two "species" are wood and foliage of the same tree. Without finding the two in actual organic connection this cannot of course be held as proven, but it seems to the writer to be highly probable.

Sequoia Langsdorfii (Brgnt.) Heer in view of the above discussion deserves special note. The name was originally applied to foliage similar to that of the living *Sequoia sempervirens*. Although in general the foliage described under this name consists of distinctly slender, linear, subparallel leaves⁴. Specimens of foliage available to the author⁵ are all very similar to that described by these authors. Other specimens have been described under the same name in which the leaves are distinctly broadened and more oval than subparallel (Dawson, 1893; Knowlton, 1899). One must conclude that either the foliage of this species was quite variable in its morphology or different workers have taken rather broad liberties in describing foliage under that caption. The former may well be the case in view of the variability noted by Knowlton in the Yellowstone.

³ Collected by the author in 1934, at an elevation of 7,000 feet, three miles northwest of the Roosevelt Lodge Ranger Station.

⁴ See: Heer, O., 1868. pl. II. Figs. 2-22; Knowlton, F. H. 1925. p. 26, pl. IX. Figs. 3-6.

⁵ No. 11460, 8986, 8987, 8923 in the Paleobotanical collections of the Botanical Museum, Harvard University. By the kind permission of Mr. W. C. Darrah.

Cupressinoxylon lamarensis Read

Fragments of wood referable to this species were collected from Big Horn Peak and Specimen Creek as well as from the Lamar River Valley where Read's type specimens were found. In our specimens from the latter locality certain histological variations from the type are notable. They are due undoubtedly to the somewhat better preservation of our material. The rays vary in height from 2 to 49 cells thus presenting a somewhat greater range than in the type where they run from 2 to 20 cells high; the pitting is mostly uniseriate although occasionally biseriate occurs. It is of interest to note that well-preserved crassulae are present (Figs. 1, 9). In the type these details were obscured due to poor preservation: The tracheids . . . failed to show details, but occasionally traces of uniseriate bordered pits are seen. Other markings which may have been present on the tracheidal wall are not preserved.⁶

The most interesting feature of our specimen is associated with the ray structure. In a number of places the radial sections show that the ends of normal tracheids are bent out of the vertical position and that they follow among the rays, thus simulating true marginal ray tracheids (Fig. 3) which are otherwise lacking. That this is not merely a mechanical effect due to radial growth seems evident from the fact that the tracheids may bend either way (centrifugally or centripetally) as shown in Fig. 4. The sporadic occurrence of bent tracheids supports the theory of the origin of marginal ray tracheids proposed by Thompson (1910). Thompson has described and figured various transitional conditions from the slightly bent tracheid to nearly normal ray tracheids in root and stem wood of the extant *Pinus strobus* and *Pinus resinosa* but to our knowledge similar transitions have never been noted in fossil woods. This presence of the feature in extinct woods which Thompson has described for living species is presented as supplementary proof of the validity of the theory.

Pityoxylon spp.

The taxonomy of the fossil pine woods of the Gallatin Fossil Forest presents a particularly difficult problem because of the wide range in their anatomical details. Woods of pine affinities are of frequent occurrence here as they are in other regions of the Park. Our collections have disclosed a considerable number of them and they can be separated into at least two forms, yet we hesitate to describe them as new species. The variation known to exist in the xylary histology of individual species and even in different parts of the wood of individual plants of living conifers is so wide that a conservative course is to be recommended in their taxonomy. Since "species" of fossil plants apply often to mere fragments which may later be assembled into a single type, they are frequently little more than filing numbers although a temporary necessity.

Both species of fossil pine wood reported by Read from the Lamar River region are described as hard or *Diploxylon pines*, and apparently on good evidence. In neither *Pinus baumani* Read nor *Pinus Fallax* (Felix) Read was tangential pitting observed in the tangential walls of the tracheids and in *P.*

⁶ Read, C. B. 1933.

Fallax "numerous canals abut directly on the primary wood and on the pith in the interfascicular areas." Our specimens appear to be, at least in part, of soft pine (*Haploxylon*) affinities. In specimen no. 232 pits are present in the tangential walls of the late spring and summer tracheids. These pits vary considerably in size as may be seen in Figs. 5 and 8. The larger pits are confined for the most part to the late spring cells while the smaller ones occur on the summer tracheids. This is a feature which is more generally associated with the soft than with the hard pines.

In neither specimen no. 232 nor 210 have dentations been observed in the ray tracheids. Specimen no. 210 is particularly well preserved and we feel safe in asserting that the smooth-walled appearance of the ray tracheids is normal and is not the result of alteration from the original state.

In view of the previously mentioned variation of structural details within the fossil and living coniferous woods and the already overburdened literature the creation of doubtfully new species of pine wood does not seem to the author necessary or justifiable. It is rather my purpose to place on record this interesting fossil florule of the Yellowstone Park and to mention the more significant anatomical details that have been observed.

SUMMARY

The fossil coniferous woods in the northwest corner of Yellowstone National Park are described in so far as they differ from those previously reported from other regions in the Park, and evidence is presented in support of Thompson's view concerning the origin of ray tracheids.

ACKNOWLEDGEMENT

Grateful thanks are due Mr. Cortland Pearsall of the Massachusetts Institute of Technology for his assistance in the collection of the silicified woods. For kindly assistance and suggestions during the course of the study I wish to thank Dr. R. E. Woodson and Dr. R. E. Torrey.

For permission to investigate this little known area of the Yellowstone I am indebted to the Chief Naturalist, Dr. C. M. Bauer for his most helpful cooperation.

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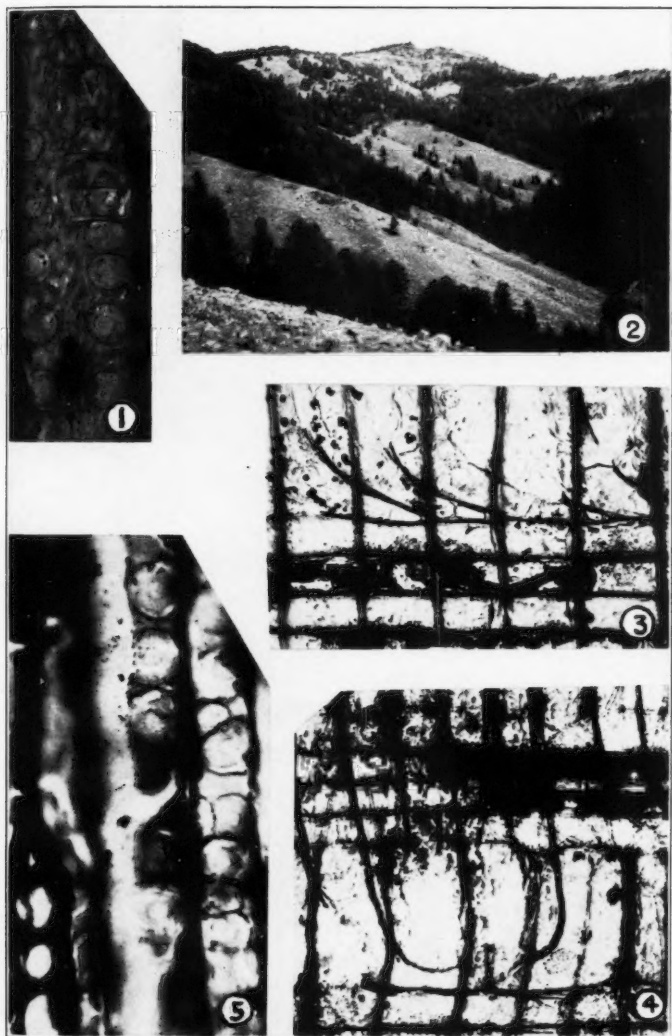


PLATE I.—Fig. 1. *Cupressinoxylon lamarensis* Read, radial wall of tracheid showing biseriate pitting and crassulae. $\times 240$; Fig. 2. Outcrop of the fossil-bearing beds—see p. 3. Figs. 3, 4. *Cupressinoxylon lamarensis* Read, radial view showing tracheids bending along the margins of the rays. $\times 200$; Fig. 5. *Pityoxylon* sp., showing pitting in the tangential walls of the tracheids. $\times 240$.

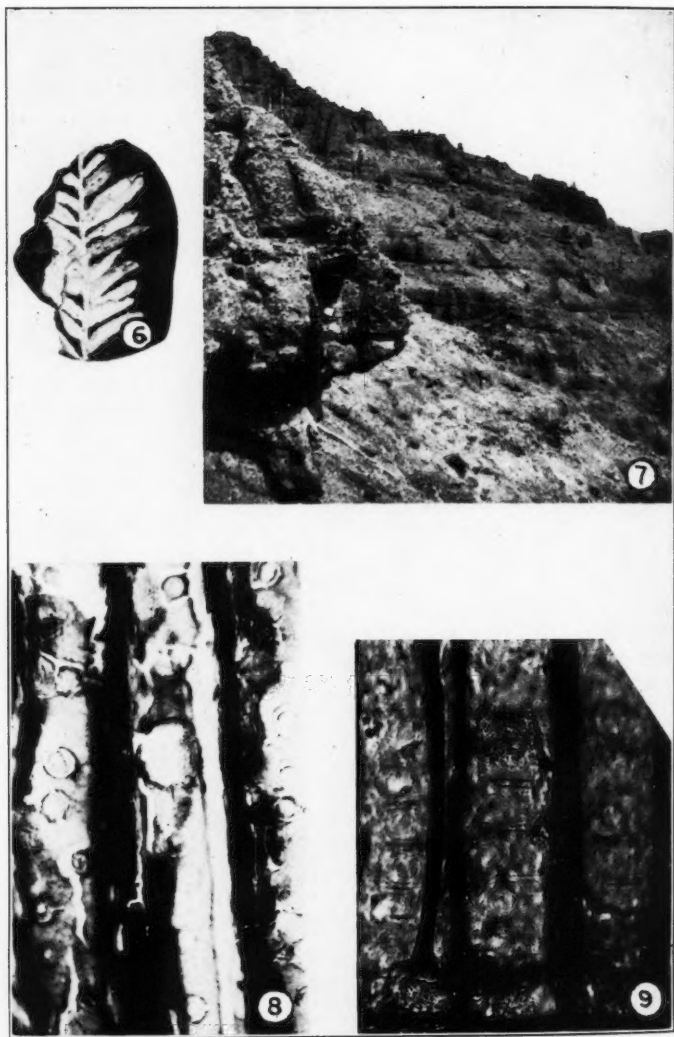


PLATE 2—Fig. 6. Foliage of *Sequoia Langsdorfii* (Brngt.) Heer. x1; Fig. 7. Close-up view of the fossil-bearing outcrop shown in the background of Fig. 2; Fig. 8. *Pityoxylon* sp., showing pitting in the tangential walls of the tracheids. x240; Fig. 9. *Cupressinoxylon lamarensis* Read, radial view. x240. Specimens of fossil wood and slides are preserved in the Botany Department of Washington University, St. Louis.

A Summary of the Fossil Crustacea of the Order Stomatopoda, and a Description of a New Species from Angola

Charles T. Berry

The present paper is the outgrowth of the author's attempt to identify a fragment of a fossil belonging to the order Stomatopoda—the description of which appears at the end of the article. It immediately became apparent that very little research had been done on the fossil representatives of this order and that the greater portion of this was the work of German paleontologists.

The author is indebted to Mr. Ernest Roschen of the Sinclair Exploration Co. for the specimen which inspired his own investigation. Also he has been greatly assisted by his colleagues in the translation of difficult passages in the foreign writings on the subject.

From the literature it is evident that there is a duplication of genera and species in the order of Stomatopoda. However, to straighten out such a condition it would be necessary to examine all the type for restudy. This proved impossible for the present work so the author has only attempted to give a short résumé of each species letting the original names stand. There are only seventeen fossil species belonging to the Stomatopoda which are grouped into nine different genera and these are found in beds from the Jurassic through the Pleistocene. Geographically these fossils are world-wide in distribution, being confined, however, to the northern hemisphere. In North America two species of different age come from California, one from North Carolina, and one from Maryland. Two species come from England and are found in beds of different age. Five different species of this order have been found in Germany, four being of the same age while the other one is somewhat younger. Only one species has been found in Italy and one in Sardinia. From Syria there has been described four species, all of the same age. The new species whose description follows comes from Angola as this Portuguese West African colony is usually called. In many cases the specimens are far from perfect and in several instances larval forms are made the basis for new species.

The earliest account of a fossil Stomatopoda was given nearly a hundred years ago when G. Münster in 1840¹ who described *Scalda pennata* from the late Jurassic (Solenhofen shale) of Germany. This sketchy description is based on three individuals which show different views. *S. pennata* had a shell which was apparently ornamented with fine tubercles and ridges and the entire animals was not more than an inch in length. In none of these specimens are there any claws the presence of which would have removed the doubts as to

Münster's correct identification. The three figures which accompany the description are very poor.

Two years later in 1842 Münster² gives a complete description of *Squilla antiqua* which had been collected from the "fish strata at Monte Bolea near Verona" and was of Eocene age. This *Squilla*, which is a little over four inches long and about $1\frac{1}{4}$ inches wide at the anterior end, lies on its ventral side. The carapace is present, showing the eyes, portions of the feelers and the second pair of feet protruding on the left side of the animal and part of the large foot on the right side. The abdominal segments are present as well as the large semi-circular telson which is flanked by fringed uropods. Münster compares this Eocene species with the living *Squilla scabricauda* Lamk. Unlike his work of two years before Münster gives a very good and clear plate of *S. antiqua* to illustrate his description.

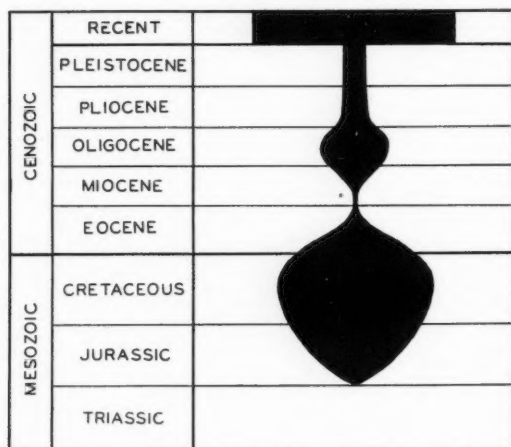


Diagram showing the geological history of the order Stomatopoda.

Brönn³ in 1848 lists both *Scalda pennata* and *Squilla antiqua*, being somewhat doubtful as to whether the former should be placed under Stomatopoda. In the second volume of the same work which was published in 1849 *Scalda pennata* is listed definitely under the Decapoda, while *Squilla antiqua* falls under the Stomatopoda.

Quenstedt in his Handbook in 1852⁴ lists *Scalda* as being as Isopod. The same error was repeated by Frischmann in 1853.⁵

While describing a small collection consisting of Insects and Holothurians from the Solenhofen, Giebel⁶ in 1857 also describes and figures what he thinks is a new genus and species of Isopoda, which he calls *Buria rugosa*. This crustacea, which is complete, shows the dorsal surface and is according to

Giebel, 11 lines long (23 mm.) by 3 lines wide (6.25 mm.) and has a very spinose surface. This specimen is carefully described and appears to Giebel as very similar to *Sculda pennata* Münster but differs, he thinks, in the shape of its head and the number of its segments. Giebel also finds that there are similarities and differences between this fossil specimen and several living Isopods in the Atlantic and the Mediterranean Sea.

Oppel, however, in 1862⁷ accepts Münster's original classification of *Sculda pennata* and *Squilla antiqua* as correct by replacing them in the Stomatopoda.

In 1865⁸ Schlüter, by describing *Squilla cretacea*, presents the second fossil belonging to this genus that had been found, the first one being *S. antiqua* described 43 years previously. *S. cretacea* consists of a well preserved thorax while the posterior segments can only be seen faintly, but clearly enough to show that these segments were without ornamentation. The appendages of the animal are badly preserved and very little can be learned from the poor illustration that accompanies the description. The specimen was collected from the Plattenkalken of Sendenhorst and is of Cretaceous in age.

Five years later in 1870 Kunth⁹ redescribes and figures *Sculda pennata* in minute detail and also describes and figures *S. spinosa* and *S. pusilla* as new species. All three of these specimens were collected from the Solenhofen deposits. In *Sculda spinosa* the dorsal side of the animal is exposed and it consists of the dorsal shield and part of the telson. Throughout the description of this new species Kunth makes numerous comparisons with *Sculda pennata*, finding that these two species differ in the form of the rostrum, sculpturing of the dorsal shield, the 15 to 19 segments and the size of the spines of the 20th. segment. *S. spinosa* as the name implies is highly ornamented with spines. In *S. pusilla* the dorsal side is exposed and this side which is nearly flat shows no evidence of spines. The animal is very small being 10.8 mm. long. However, Kunth does not consider it as a young of the other two species from these deposits. Kunth likewise goes into a discussion as to the systematic arrangement of these animals citing authors on both the fossil and living species. The material on which Kunth worked was loaned to him from the München paleontological collection and the Berlin University collection. Kunth had 24 examples of *S. pennata* to work with ranging from 46 mm. to 22 mm. long. Only 3 examples of *S. spinosa* whose size ranged from 35 mm. to 31.3 mm. and only one example of *S. pusilla*. Kunth states that Giebel's *Buria rugosa* is no other than *Sculda pennata* thus discarding entirely the name as given by Giebel.

In 1872 Schlüter¹⁰ records the finding of *Sculda laevis* from the Upper Cretaceous beds near Lebanon. He endeavors to use this specimen in the age determination of the beds in which it was found, but finds that there is not enough known about these Stomatopoda for this purpose. Schlüter does not describe or figure this specimen, he only names it. The generic name of this species was changed from *Sculda* to *Pseudosculda* in 1886 by Dames, as will be mentioned later.

Two years later in 1874 Schlüter¹¹ minutely described and illustrated *Sculda laevis* of which he had previously only recorded the finding. Careful measurements are given as to the size of portions of the animal—its full length being 38 mm. and its greatest width 10 mm. Schlüter is doubtful as to just where to place this fossil, for he says that the cephalothorax is more closely related to *Squilla* than to *Sculda*; while certain characters of the telson indicate its relation to *Sculda*. He feels that when larger and more perfect specimens are found *Sculda laevis* will form the type of a new genus.

In 1879 H. Woodward¹² describes and figures *Squilla wetherelli* from a phosphatic nodule of the London Clay (lower Eocene). This specimen, which shows the dorsal side, consists of "five well preserved segments" portions of the carapace with "traces of the thoracic appendages and those of the xxth. segment, preceding the telson." He compares the fossil species with a number of living ones from the vicinity of Great Britain (*Pseudosquilla Lessoni*, *Gonodactylus chiragra*, *G. cultrifer*, *Squilla mantis*, and *S. desmarestii*) and finds that it is closest to *Squilla desmarestii*. In part two of the same article Woodward describes and figures a specimen which he names *Necroscilla Wilsoni*, but is doubtful as to whether it belongs to the order Stomatopoda or Isopoda. It has never been considered as belonging to the former order since the time of Woodward and we shall not consider it otherwise here. In the third part of this article Woodward describes a specimen from the valley of Hakel in Lebanon, Syria, which he identifies as *Squilla Lewisii*. This specimen, which is embedded in limestone, exposes to view the right side, and practically the entire animal is preserved. The shell of this *Squilla* is smooth, showing no ornamentation. Along with this description Woodward mentions *Sculda pennata* Münster which he wishes to rename *Squilla pennata*. Both *Squilla Lewisii* and *Sculda pennata* are clearly illustrated.

In this same year communications from Woodward¹³ were read before the Geological Society on May 28. In these communications he very briefly describes *Squilla wetherelli*, *Necroscilla Wilsoni* and *Squilla Lewisii*. In all probability this account preceded the above more complete description even though the date is the same.

Hilgendorf in 1883¹⁴ superficially describes a fossil which he states is the larva of *Squilla*, basing this fact on the similarity with living *Squilla* larvae which he has seen. This fossil larva comes from the Cretaceous beds at Sahel Alma in Lebanon. Hilgendorf in closing hopes that W. Dames will thoroughly describe additional larval material.

In a long article, W. Dames reviews in 1886¹⁵ all the previous work on the order Stomatopoda and adds several new species to the then known short list of these Crustacea. He describes in great detail two specimens of *Sculda syriaca* which had been collected from the Upper Chalk near Hakel in Lebanon. In one specimen the shield is preserved while in the other the tail part with its appendages. Dames presents in great detail the reasons why he places these specimens under the genus *Sculda* and he compares their sculpturing to that of *Sculda pusilla* Kunth, *Sculda pennata* Münster and *Sculda*

spinosa Kunth. He also discusses fully the importance of the appendages of the tail fin upon which Kunth and Schlüter hold adverse opinions in connections with the genera *Squilla* and *Sculda*. Unfortunately Dames bases a large portion of his conclusions upon the illustrations in earlier literature and not upon actual study of the specimens. Dames also proposes to set up the genus *Pseudosculda* as well as the family *Pseudosculdidae* to include the specimen which Schlüter called *Sculda laevis*, basing this new genus upon the structure of the tail fin.

Dames also describes in detail, and makes comparisons with the living forms, certain specimens to which he gives the name of *Pseuderichtus cretaceus* claiming that these specimens are the larvae belonging to the order Stomatopoda. Likewise he describes another type of larvae giving it the name of *Protogoea hilgendorfi*. Both of these types of larvae come from the Upper Chalk of Sahel Alma in Lebanon.

In this work there is included a table showing various distribution of the Crustacea from Lebanon as well as a table to show the geological distribution of certain families of Stomatopoda.

In 1888 Oppenheim¹⁶ from a collection of 23 specimens of larvae from the Solenhofen beds creates a new genus and species which he calls *Clausia lithographica*. The specimens are somewhat distorted, the largest being about 45 to 50 mm. long, while of the six figured the largest is 15 mm. long by 7 mm. wide. Even though the specimens are lying on their sides he can make out ten abdominal segments which immediately excludes it from the Decapods. This difference is also indicated by the number of leg pairs, long anterior swimming feet, lack of telson and the characteristic thoracic-abdominal covering. Oppenheim finds that this fossil larva differs from those of the living Stomatopoda larvae and that it does not belong to any of the previously described fossil larvae. He also goes into a lengthy discussion concerning the larvae of Stomatopoda and Decapoda, concluding that the exact placement of *Clausia lithographica* will be better known as more work is done on these fossil larvae.

From the Miocene beds at Sardinia, Lovisato collected and described in 1894¹⁷ the nippers of the second pair of maxillaries of a species of Stomatopoda. The beds from which these fossils came are discussed in great detail as well as a lengthy comparison of the fossil *Squilla* with some of the recent ones from the Ardiatic sea. Lovisato has given these nippers the name of *Squilla miocenica* and includes in this article three poor illustrations. Throughout the paper the author laments the lack of cooperation he received from other scientists and his lack of literature which handicapped the work.

Jukes-Browne in 1900¹⁸ lists with the other fossil of Cretaceous age from Britain, *Squilla McCoyi* Seeley. In his list this *Squilla* is placed under the Decapoda. *Squilla McCoyi* never seems to have been fully described for no other mention of this species has been found in the literature.

Walther in 1904¹⁹ published a list of fauna from the Solenhofen beds

and listed under the phylum Arthropoda *Skulda pennata*, *S. pussilla*, and *S. spinosa*. It is gratifying to observe that Walther lists these three species under the order Stomatopoda. No remarks are made about any one of these three species of Skulda.

In Kemp's well rounded work of 1913²⁰ on the Stomatopoda from the Indo-Pacific region he mentions in his general discussion the fossil Stomatopoda, giving only a brief résumé of various genera and disregarding the different species. This work is one of the best dealing with living Stomatopoda and to one interested in the subject it will prove invaluable.

The most recent writings on fossil Stomatopoda are the papers of Miss M. J. Rathbun, one in 1926 and one in 1935. In 1926²¹ she describes and figures two representatives of the Stomatopoda. Of these *Chloridella sonomana* (Chloridella of Miers having replaced Fabricius' Squilla) is represented by portions of the abdominal somites and fragments of the carapace. The specimen was collected from the Pliocene beds of Sonoma County, California. There seems to be some doubt in Miss Rathbun's mind as to the exact placement of this species because the diagnostic anterior and posterior ends are lacking. Also from California in San Luis Obispo County, Miss Rathbun describes and figures *Pseudosquilla adelaidensis* from middle Miocene beds. This specimen likewise is represented only by portions of the abdominal somites which are lacking in sculpturing. The genus *Chloridella* is listed as coming from the Jurassic, Cretaceous, Eocene, Miocene, Pliocene, and Recent. While the genus *Pseudosquilla* is limited to the Miocene and Recent.

In Miss Rathbun's work of 1935²² the arrangement is based upon the age of the deposits, each period being dealt with separately. In the first part of her article are lists of the various species,²³ under the Miocene Stomatopoda is *Gonodactylus oerstedii* while under the Pleistocene ones is *Chloridella empusa*. In the stratigraphic discussion a brief statement of a fragment of *Gonodactylus oerstedii*²⁴ is given and its occurrence is as from the St. Mary's formation of Nash County in North Carolina. Of *Chloridella empusa*²⁵ only the telson and one terminal article of the second thoracic appendage is reported from the Talbot formation of St. Mary's County, Maryland. Neither of these two species is described or figured.

Such textbooks as Zittel,²⁶ Lankester,²⁷ Calman²⁸ and others do not add anything to our knowledge of the various fossil species of Stomatopoda. Instead they reiterate statements made by earlier authorities on this order, oftentimes including copies of the original figures which are generally poor. Thus it is not necessary to consider accounts of this type of publication in the present discussion.

In the September issue of the Journal of Paleontology—H. W. Scott* describes a new genus and species of Stomatopod from the Heath shale (Mississippian) of Montana.²⁹ The most perfect of the two specimens found

* Note: This article came to the attention of the author too late to more than mention it in the present paper.

is used as the type. The new species has been named *Squillites spinosus* and is placed under the family Squillidae. The type specimen consists of "Parts of the first and second antennae, the monodactylus maxillipede, and most of the appendages on the twentieth somite are preserved, as well as the abdomen, thorax and carapace." The specimen is very small and the illustration leaves much to be desired. Scott is apparently unaware of Rathbun's papers of 1926 and 1935 in which the family Squillidae has been replaced by Chloridellidae.

In the fall of 1932 Ernest Roschen, then working along the Cuanga River, Quissama District, Angola, collected the posterior portion of a Stomatopod. This specimen finally was placed in the hands of the author for identification and the following description is the result. The region from which the specimen was collected is 9° to 10° south latitude and between $13^{\circ} 30'$ to $14^{\circ} 30'$ east longitude.

The material in which the specimen is preserved is a coarse grained calcareous sandstone being irregularly partly cream and partly reddish in color, indicating the possibility of a shallow water deposit. Since the actual specimen appears to lie across the bedding plain of the limestone, as though it had been preserved in its hole, one would be justified in concluding that this deposit was laid down in littoral waters. This is proven by the fact that out of the 139 living Stomatopoda today only eleven have ever been found below 100 fathoms.³⁰ This calcareous sandstone is called the Cuanga Chalk from the Cuanga River along which it outcrops and is of Cretaceous age. Beds of Cretaceous age outcrop for about 50 miles along this river in the vicinity of Dondo.³¹

Chloridella angolia sp. nov.

Fig. 1

The specimen which consists of the posterior portion of a Stomatopod is composed of the fourth to eighth abdominal somites inclusive, the telson and both the right and left pairs of exopodites and endopodites—the processes from the peduncle of the uropod are either lacking or more probably obscured by the rest of the uropods. The specimen is an intaglio of the dorsal side with the actual shell material preserved, though badly cracked by crushing.

Starting at the anterior end of the specimen there is the greater portion of the fourth abdominal somite preserved though the anterior right corner is lacking. The right marginal carina of the fourth somite is indistinct while the left one is absent. The intermediate carinae appears as deep grooves extending the entire distance across the somite. The submedian carinae do not appear as two complete parallel grooves, but are interrupted by a raised area.

The fifth abdominal somite is like the preceding one but the submedian carinae are somewhat deeper while the left marginal carina is very pronounced.

The sixth abdominal somite is like the two preceding ones. Its right hand margin is distorted while its left one is perfect. The intermediate carinae tends to flare out towards the posterior edge of the somite.

The seventh abdominal somite is like the fourth, fifth, and sixth, with its

marginal, intermediate and submedian carinae all present. The lateral margin rounds in to the posterior edge of the somite unlike that of the preceding ones which give the illusion of spines. The intermediate carinae flare near the posterior margin.

In the eighth the submedian carinae appear as continuous, deep grooves tending to converge towards the posterior margin of the somite. The intermediate carinae converge towards each other. The lateral margins of the somite rounds into the uropods. This somite is shorter than the four preceding ones.

Separating each abdominal somite is a deep furrow.

The telson which is broad has a rounded posterior margin which is very

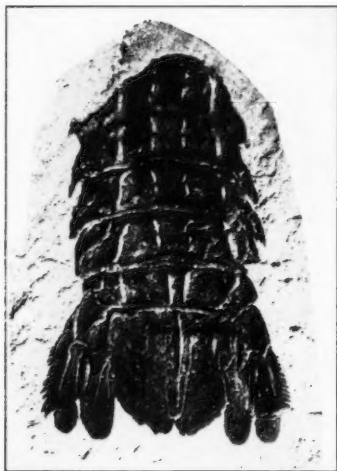


Fig. 1. Abdominal somites of *Chloridella angolia*, x1.

irregular due to the breaking apart of the shell. In the center of this margin is a deep V-shaped sinus whose lobes could be designated as submedian teeth. Otherwise the jagged margin does not show any definite teeth. The median carina of the telson appears as a broad groove which is deeper near the anterior end, becoming shallow towards the posterior margin. Flanking both sides of this carina is the submedian carina of the telson which is much less pronounced and whose posterior ends curve in and unite just anterior of the margin of the telson. This telson appears to be longer than broad even though its lateral edges are hidden by the uropods. The shell material of the telson is greatly cracked as shown by the fine lines which cross this portion of the fossil.

Both the right and left uropods are somewhat obscured by their three

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constituents overlapping each other. The spines on the basal prolongations cannot be discerned in both uropods. In the right uropod the exopodite and endopodite can be clearly seen. The rounded paddle of the exopodite is half as long as the second joint. No spines are present on this paddle while 12 spines can be distinguished on the outer edge of the second joint. The large paddle of the endopodite also has a rounded posterior end which extends further posteriorly than either the telson or the exopodite. The left uropod is similar to the right one, except that on the second joint of the exopodite there are present only 10 spines. The reniform shape of the paddle of the endopodite stands out better than in the right uropod, being somewhat broader in the left one than in the right. Whether the spines on the outer edges of the second joints of the exopodites are movable cannot be discerned in this specimen.

Measurement on middle line	
4th abdominal somite	7.0 mm.
5th abdominal somite	6.5 mm.
6th abdominal somite	7.5 mm.
7th abdominal somite	8.5 mm.
8th abdominal somite	7.5 mm.
Telson	17.5 mm.

Greatest width	
4th abdominal somite	20.0 mm.
5th abdominal somite	24.0 mm.
6th abdominal somite	27.0 mm.
7th abdominal somite	28.0 mm.
8th abdominal somite	25.0 mm.

Length of second joint of exopodite of left uropod	10.5 mm.
Length of paddle of exopodite of left uropod	3.5 mm.
Length of paddle of endopodite of left uropod	14.0 mm.

The systematic placement of this fossil is somewhat doubtful because many of those characters which are used to separate the genera of the Stomatopoda are absent in this specimen. Kemp³² separates the families Scudidae and Squillidae by the fact that in the former the exopodite of the uropod is composed of only a single segment, while in the family Squillidae the exopodite is composed of two distinct segments. The exopodite of the specimen in question is distinctly composed of a short paddle and a long second joint thus placing it in the family Squillidae.

Miss Rathbun thinks that the family Squillidae of Miers should be replaced by Chloridellidae and has used this in her classification of fossil forms.³³ Likewise she replaces the genus Squilla by Chloridella. These two genera have long been considered as very closely related or as the same. This is shown by the following statement which W. K. Brooks makes, "It is quite impossible to draw any line to separate the genus Squilla from the genus Chloridella, and all the species must therefore be associated in a single genus Squilla."³⁴

In the generic identification of the specimen from Angola one is faced with a very perplexing problem for the characters, such as the form of the

dactyles of the raptorial claws, the shape of the eyes, rostrum, carapace and marginal spines of the telson which are used for identification are all lacking in this specimen. There remains only the sculpturing on the abdominal somites and telson and the proportions of various parts of the shell to work with. The sculpturing on the abdominal somites is indicative of the genus *Squilla*. The telson appears to be longer than it is wide though the exact width cannot be measured because of the overlapping of the uropods, and this is also indicative of *Squilla*. Thus this specimen belongs to the genus *Squilla* or more rightly *Chloridella* as sanctioned by current usage.

Even though the present author hesitates to set up a new species on such fragmentary remains he feels justified in doing so since this is the only fossil specimen of *Stomatopoda* so far found in Africa or even in the southern hemisphere. Therefore, this *Stromatopod* has been given the name *Chloridella angolia* C. Berry, the specific name being taken from the country in which the specimen was found.

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GEOLOGICAL DEPARTMENT,
JOHNS HOPKINS UNIVERSITY,
BALTIMORE, MD.

Dispharynx pipilonis, a New Spiruroid Nematode from the Red-eyed Towhee

[*Pipilo erythrophthalmus erythrophthalmus* (Linn.)] (1, 2)

O. Wilford Olsen

During the course of his studies on the life history of the red-eyed towhee, Mr. Roger Barbour of Morehead State Teachers College, Kentucky, collected a number of nematodes from the proventriculus which he kindly sent to the author for identification. Upon examination, they were found to be an undescribed species of the genus *Dispharynx* Railliet, Henry, and Sisoff, 1912, for which the name *Dispharynx pipilonis* n. sp. is proposed.

Dispharynx pipilonis n. sp.

Specific diagnosis: Stout white worms. Cuticular striae fine, about 4μ apart. Four wavy cordons which extend from lips to region of union of muscular and glandular oesophagi, recurrent for one-third to two-thirds their length. Post-cervical papillae simple, located between cordons just cephalad from posterior extremity. Two simple lips.

Male: Length 4.6-5.6 mm., width 233-283 μ . Buccal capsule 80-120 μ long; muscular oesophagus often convoluted, length 316-500 μ , glandular oesophagus 1.6 mm., combined length of oesophagi 1.9-2.1 mm. Nerve ring 200-260 μ from anterior end. Excretory pore just anterior to posterior limit of cordons. Cloaca 252-274 μ from tip of tail. Spicules dissimilar, right navicular in shape, anterior half slender with a terminal hook extending ventrad and a sharp ventral spine followed by a deep broad incision, on the right side of the spicule is a curved process cephalad from posterior margin of incision (see figure), length 104-160 μ , width 20-24 μ ; left spicule simple in shape, long and slender, length 428-484 μ . Caudal end of body tightly coiled, usually about $1\frac{1}{2}$ coils, ventral surface of caudal part of body with strong longitudinal ridges; caudal alae narrow, margins thickened. Nine pairs of caudal papillae, four of which are preanal and five postanal. All papillae are stalked except last pair which is located at tip of tail. Of the preanal papillae, the first and third pairs have long stalks and the second and fourth pairs have short stalks; of the postanal papillae, the first and third pairs have short stalks and the second and fourth have long ones..

1 Paper No. 1643 of the Scientific Journal Series of the Minnesota Agricultural Experiment Station, St. Paul.

2 A joint contribution by the University of Minnesota Agricultural Experiment Station and the Minnesota Department of Conservation, Division of Game and Fish.

Female: Length 4.5-5.8 mm., width 483-549 μ . Buccal capsule 108-148 μ ; muscular oesophagus strongly convoluted, united with glandular oesophagus 260-400 μ caudad from anterior end of body; glandular oesophagus 1.4-1.8 mm. long. Several large cells and usually fewer small ones surround anterior part of muscular oesophagus. Cords 433-616 μ , recurrent branch one-third to two-thirds length of other; five to seven loops. Nerve ring not seen. Excretory pore opens just anterior to posterior limit of cords. Vulva 0.933-1.3 mm. from tip of tail, divides body approximately as 3:1. Vagina runs obliquely cephalad for about 330 μ and then turns abruptly caudad. Tail 140-160 μ long, smooth, and blunt. Eggs 36-44 by 22-24 μ .

Type—United States National Museum, Helm. Coll. No. 9207; *Co-types*: V.2056 Helminthological Collection of Division of Entomology and Economic Zoology, University of Minnesota.

DISCUSSION

Dispharynx pipilonis is closely related to *D. stonae* Harwood, 1933. *D. spiralis* (Molin, 1858) and *D. emberizae* Yamaguti, 1935. It differs from *D. stonae* in that the latter has a long right and a short left spicule; from *D. spiralis* whose female has a tail terminating in a sharp spine; and from *D. emberizae* in the shape of the short right spicule. The anterior half of the right spicule of *D. pipilonis* is very slender, forming a hook which points ventrad and a sharp ventral spine, while in *D. emberizae* both the hook and spine are lacking.

The following key has been adapted from Cram (1927:237) and includes the five species that have been described since its publication.

KEY TO THE SPECIES OF DISPHARYNX

1. From *Falco minutus* or *Rhamphastos vitellinus*, inadequately described..... 2
 From hosts other than above, adequately described..... 3
2. Lips very small; cords short; from *Falco minutus*.....
 *Dispharynx capitata* (Molin, 1860)
 Lips large; cords long; from *Rhamphastos vitellinus*.....
 *Dispharynx crassissima* (Molin, 1860)
3. Male with 7 pairs of postanal papillae; from *Ajaja ajaja*, *Platalea ajaja*.....
 *Dispharynx magnilabiata* (Molin, 1860)
 Males with less than 7 pairs of postanal papillae..... 4
4. Male with 4 pairs postanal papillae..... 5
 Males with 5 pairs postanal papillae..... 6
5. Longer spicule twice the length of the shorter; from *Falco ater*.....
 *Dispharynx rectovaginata* (Molin, 1860)
 Longer spicule 2.79 times the length of the shorter; from Java cock.....
 *Dispharynx notoi* Smit, 1927
6. Vulva near middle of body..... 7
 Vulva in posterior third or fourth of body..... 9
7. Vulva anterior to middle of body; longer spicule three times length of shorter;
 from *Gallus gallus*.....*Dispharynx nasuta* (Randolphi, 1819)

- Vulva near middle of body but never anterior to it 8
8. Longer spicule (260 μ) 2.25 times the length of the shorter one (115 μ); males 6.5 mm. long, females 10-11 mm.; lips each with a large papilla at base; from *Carine noctua glaux*. *Dispharynx noctuae* (Seurat, 1913)
- Longer spicule (right, 0.950-1 mm.) 38 times the length of the shorter one (left, 24-27 μ); males 10-11.6 mm. long, females 14-15.5 mm.; from white hawk (? *Astur novae-hollandiae*). *Dispharynx fieldingi* Baylis, 1934
9. Right spicule 240 μ long, thick and falciform, left 865 μ long, slender, pointed at tip, not alate; from *Carrulus glandularius cervicalis*. *Dispharynx laplantei* Seurat, 1919
- Short spicule navicular in shape, does not exceed 160 μ in length, long spicule slender, reaching 520 μ 10
10. Right spicule longer (385 μ) than left (154 μ); from *Thyrothorus ludivicians*. *Dispharynx stonae* Harwood, 1933
- Right spicule shorter than left by at least 2 times 11
11. Female tail 120 μ long, terminating in a small spine; right spicule 150-200 μ , left 400-520 μ ; from gallinaceous birds. *Dispharynx spiralis* (Molin, 1858)
- Female tail longer, not terminating in a spine 12
12. Anterior half of right spicule with a terminal hook extending ventrad and a sharp ventral spine followed by a deep, broad incision; males 4.6-5.6 mm., females 4.5-5.8 mm.; female tail 140-160 μ ; from *Pipilo erythrophthalmus erythrophthalmus*. *Dispharynx pipilonis* n. sp.
- Anterior half of right spicule without a terminal hook but straight, no ventral spine; males 6-8 mm. long, females 6.4-7.7 mm.; female tail 140 μ ; from *Emberiza spodocephala personata*. *Dispharynx emberizae* Yamaguti, 1935

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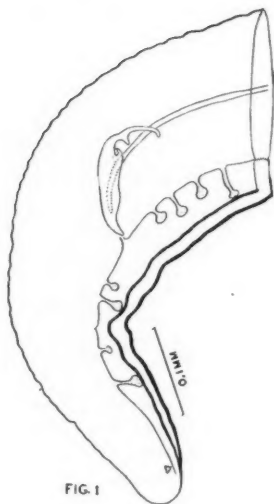


FIG. 1

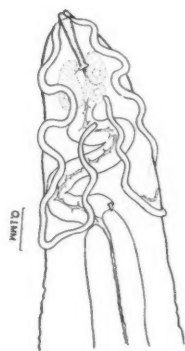


FIG. 2



FIG. 3

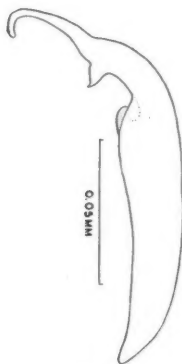


FIG. 4

Fig. 1. Dextral view of the caudal end of the male; Fig. 2. Dextral view of the anterior end of the female; Fig. 3. Dextral view of the vulva and vagina; Fig. 4. Sinistral view of the right spicule showing the details.

The Life Cycle of the Frog Bladder Fluke,

Gorgoderina attenuata Stafford, 1902 (Trematoda: Gorgoderidae)

John S. Rankin, Jr.

Introduction

A survey of many ponds in western Massachusetts for their cercarial fauna has revealed a high infestation of the bivalve mollusc, *Sphaerium occidentale* Prime with a gorgoderid cercaria. Tadpoles of *Rana sylvatica* LeConte, *R. clamitans* Latreille, and *R. pipiens* Schreber from these ponds are heavily infested with cysts which, on examination, seemed to be identical with this gorgoderid cercaria. Adult frogs and newts (*Triturus v. viridescens*) in this area are commonly infested with *Gorgoderina attenuata* Stafford, 1902. With these field observations as a background, a series of experiments were undertaken to establish definitely the life cycle of this species of bladder fluke. The consequent results indicate that the life cycle is as predicted from the result of the field survey.

Although bladder flukes have been known to occur in amphibia for quite some time, as far as can be determined this is the first report on the complete life history of a member of the genus *Gorgoderina*. Previous work has been concerned largely with species of *Gorgoderina*. Flukes from the bladder of *Rana esculenta* were reported as far back as 1785 by Loschge, and subsequently named *Distomum cygnoides* by Zeder (1800). Looss (1902) separated this group of trematodes into two genera on the basis of number of testes, *Gorgoderina* with nine, and *Gorgoderina* with but two testes. These genera have been reported in North America by Leidy (1851), Bensley (1897), Stafford (1902), Cort (1912), Guberlet (1920), Harwood (1932), Ingles and Langston (1933), Krull (1935), Ingles (1936), Rankin (1937), Odlaug (1937), and Olsen (1937). Olsen presents a key to the fourteen species of *Gorgoderina* that have been so far described. Two species of *Gorgoderina* have been recorded.

The first studies on the life history of these flukes were carried out by Ssinitzin (1905), who described the larval stages of several, and traced the development of these larvae to adult worms. He found the cercariae to be of the cysticercous type and concluded that the large tails of the cercariae enabled the worms to be caught and eaten by insect larvae which, in turn, became infected. By rather incomplete experiments he showed that larval *Epitheca* served as host for the metacercaria of *Gorgoderina loossi*, and that larval *Agrion* served as host for metacercariae of *Gorgoderina varsoviensis*. On feeding these infected second intermediate hosts to adult frogs, adult worms of the respective species were recovered. Lutz (1926) reported the intermediate hosts of a species of *Gorgoderina* as follows: cercariae in bivalves, *Cyclas* and *Psidium* or *Sphaerium*; metacercariae in dragonfly larvae. The first life history of frog bladder flukes to appear in the United States was

that of Krull (1933, 1935) on *Gorgoderina amplicava* Looss. He found *Musculum partumicum*, *Helisoma antrosa*, and *Rana clamitans* and *R. catesbeiana* as first and second intermediate hosts and definitive hosts, respectively.

Materials and Methods

Material for this study was collected from various ponds around Amherst, Massachusetts. For the life cycle study itself, material raised in the laboratory was used. *Sphaerium occidentale* was isolated in finger bowls and observed for cercariae and young *Sphaerium*. These young molluscs were transferred to sterilized aquaria and raised to adults. By artificially inseminating *Rana clamitans* eggs, obtained by injecting pituitary extract into female frogs, parasite-free tadpoles were available for infection experiments. Some of these tadpoles were raised to adults, as were larval *Triturus* collected in a pond free of *Gorgoderina* species. These methods insured uninfected experimental animals. As a double check, however, controls were maintained.

Tadpoles were placed in fingerbowls with molluscs that were shedding cercariae and killed at various intervals to follow the process of infestation in the second intermediate host. Cysts were dissected from tadpoles and placed in fingerbowls with adult hosts. After recovery of adult worms, ripe eggs were placed in stender dishes with *Sphaerium* and the development of miracidia into sporocysts, and finally cercariae, followed.

All fluke material was studied both alive and preserved. Intra-vitam stains were found to be of practically no value except neutral red in studying miracidia. Flukes were killed in Conant's fixative, stained in borax-carmines precipitated with hydrochloric acid, cleared in cedarwood oil, and mounted in damar. By drawing the fixative under the coverslip with filter paper, uniform fixation without distortion was obtained.

The writer wishes to express his appreciation to Mr. C. F. Holthausen and Mr. W. R. Merchant for their interest and help in collecting material for this study.

Experiments

All of these experiments have been repeated several times. Only a few typical ones are reported here.

1. Experiments with first intermediate hosts.

Specimens of adult *Gorgoderina* from experimentally infected frogs were placed in stender dishes in tap water, pond water, distilled water, and Amphibian Ringers' Solution. Only those in pond water shed eggs. Even when kept for several hours in the other media flukes merely became swollen and then began to disintegrate. It was found that by teasing individual worms apart, hundreds of ripe and near-ripe eggs could be obtained which would hatch in a comparatively short time (ten minutes to two hours). A single specimen of laboratory-raised *Sphaerium occidentale* was placed in each stender dish with hatching miracidia. Observed under the dissecting microscope, these miracidia were seen to swim rapidly about, with no apparent definite course. On brushing against the mollusc, they became motionless, remained for a

moment or so, and then resumed their aimless swimming. No active penetration from the outside was observed at any time. On swimming opposite the molluscs' incurrent siphons, however, the miracidia were swept into the mantle cavity. This, as far as can be determined, is the only method by means of which the first intermediate host becomes infected. Many hosts placed with hundreds of miracidia died, whereas those with but twenty-five to fifty larvae survived. All controls survived. It would seem, therefore, that heavy infestation with miracidia may be a contributing factor in the consequent death of the host. Dissection of molluscs so infected has shown some miracidia free in the mantle cavity, some actively penetrating the proximal ends of the gills, and some wholly within the gills, cilia sloughed, slightly elongated, developing into the mother sporocyst.

2. Experiments with the second intermediate host.

At first, laboratory-raised tadpoles of *Rana clamitans* and *R. pipiens* were placed in fingerbowls with cercariae shed from *Sphaerium* naturally infected, to determine if these animals were normal hosts. On finding the tadpoles soon heavily laden with cysts, cercariae from experimentally-infected *Sphaerium* were used, to complete the experimental life cycle. The tadpoles are bottom-feeders, subsisting on algae, organic debris, etc. The large tail of this cercaria is picked up with other material and taken into the digestive tract of the tadpole. On dissecting the tadpoles at different intervals, cercariae still in the tail were found in the stomach. Slightly posterior to the stomach, however, cercariae had escaped from the tail stem and were actively migrating up and down the intestine. In five cases, cercariae were observed penetrating the intestinal wall just below the stomach. Free cercariae were found in the body cavity, with large numbers of cysts around the heart and liver. In all of these, only the hyaline cyst of parasite origin was formed. Consequently, the cysts were not firmly attached, but easily removed with the slightest push of the needle.

Specimens of various species of insect nymphs, gastropods, and other bivalve molluscs were placed with cercariae. In only one out of twenty *Pseudosuccinea columella* Say was a single cyst recovered. Apparently this gastropod may serve as a second intermediate host, but, from these experiments and from finding only occasional such natural infestations, this host is certainly not a normal one. Larval *Triturus* become lightly infected, never accruing the large number of cysts recovered from *Rana* tadpoles.

3. Experiments with definitive hosts.

Cysts were dissected from tadpoles and placed in fingerbowls, each containing a laboratory-raised adult *Rana clamitans* or a *Triturus*. These hosts were killed at intervals to determine the path of intestinal infestation. All hosts picked up cysts and became infected. Although the exact number of cysts were not always counted, still from the number of excysted flukes recovered, it would seem as though practically every cyst survives in the definitive host. Cysted and excysted metacercariae were recovered in the stomach. Below the stomach, young worms, free of their cyst were found migrating toward the posterior end. In two hosts none were found in the intestine, but on examin-

ing the kidneys and ureters, were recovered in large numbers. No immature worms were ever observed in the body cavity. Infected tadpoles were placed in fingerbowls with frogs and newts and were soon eaten, thereby establishing the fact that these animals do become infected by eating their young.

Infestation Found in the Field

A survey of aquatic invertebrate fauna in western Massachusetts has established the fact that tadpoles are the natural second intermediate host for this species of bladder fluke. Dragonfly and damselfly larvae are entirely negative as are bivalve molluscs. Occasionally a cyst or two are found in *Pseudosuccinea columella*, but have never been observed in other species of gastropods. In one pond, 100% infection, with an average of 263 cysts per tadpole, has been recorded. Practically every pond surveyed contains a few infected hosts. It may be of interest to note that specimens of the genus *Gorgoderina* have not as yet been found in any of the adult hosts examined.

Description of Stages in the Life History

1. *Miracidium*.

The first larval stage of *Gorgoderina attenuata* resembles in form that of many described miracidia (Price, 1931; Hunter and Hunter, 1935; etc.). It is usually pyriform although it may modify its shape greatly by contraction and extension. The greatest width is near the posterior margin of the anterior body third. Average length of ten specimens is 0.072 mm.; average width, 0.039 mm.

Miracidia may be observed actively surging back and forth within the eggs located in the distal uterine coils of the mature worm (Fig. 1). Within a few minutes after the eggs are shed, miracidia may be found swimming vigorously about. Some have been observed in active motion 18 hours after hatching. After this time, however, activity tends to decrease, and by 24 hours most larvae are dead.

Practically the entire surface of the miracidium is covered with long cilia (0.013 mm.) which arise from 24 epidermal cells (Fig. 2). These cells are arranged in four transverse rows. The first row consists of 6 cells, comparatively small, and roughly triangular in shape. The second row contains 8 cells, bluntly rounded and nearly rectangular. The 6 cells in the third row are much larger than those in the anterior two rows and are also bluntly rounded and rectangular. The posterior row consists of 4 large cells, roughly rectangular, bases toward the anterior end. Distance between rows is about the same in all cases and these spaces do not bear cilia. Cilia are likewise absent from the anterior and posterior tips although the backward sweep of cilia from the posterior cells tends to cover the posterior tip. An *en face* view shows these cells to good advantage and the differentiation into "plates" may be more easily recognized. These cells are filled with tiny refractive granules and stain deeply with neutral red. A clear, oval nucleus lies in the center of each cell.

The clear, non-ciliated areas between the epidermal plates are the exposed parts of the sub-epithelium over which lie the plates. This sub-epithelium

consists of a single layer of comparatively large cells, the nuclei of which can be observed only with difficulty. This layer tends to bulge slightly between the epidermal plates, but at no time does it form any distinct papillae. Since, after penetration into the gills of the clam, the epidermal cells are sloughed, the sub-epithelium apparently becomes the wall of the mother sporocyst. This casting of epidermal plates has been observed by various workers (Leuckart, 1882; Barlow, 1925; Van Haitsma, 1931; Price, 1931).

Although the anterior tip may be extended and retracted forming a more or less distinct protrusion, no evidence of a typical apical papilla, observed by Price (1931) and Hunter and Hunter (1935), was found. A sac-like structure extends posteriorly from the anterior tip and apparently opens to the outside by a small apical opening (Fig. 3). This is the so-called "gut," but whether it is glandular or actually a true gut is not certain. It is characterized by its clear, empty space, containing no granular material. Five large bodies surround the gut, two lateral pairs and a single posterior one; these are very granular and may represent apical glands observed by Price (1931). No trace of a nervous system was identified, although a light area posterior to the gut occasionally noticed may have been the fundament of this system.

The excretory system consists of a single pair of very large flame-cells, easily observed in a miracidium still within the egg (Fig. 1). Each flame-cell is located near the median plane just anterior to the middle of the body. A duct from each extends posteriorly a short distance, loops forward to in front of the flame-cell, turns posteriorly again, and then empties by a small lateral pore situated between the third and fourth rows of epidermal plates (Fig. 3).

Although the whole body of the miracidium is filled with large refractive droplets, a mass of cells near the posterior end (Fig. 3) probably represents the germ balls. These cells maintain position in spite of the constant contractile body-movements. No fibre-like filaments attaching them to the body-wall as described by Price (1931) were observed.

As a whole, the miracidium of *Gorgoderina attenuata* appears to be much less complex than those described for other genera of trematodes. No lateral processes or papillae, nor cephalic gland ducts of any kind were recorded. Eyespots and a well-developed nervous system seems likewise to be lacking.

2. Mother Sporocyst.

The miracidium penetrates the gills of the clam and comes to rest between the gill lamellae. As it enters the clam tissue, the epidermal cells are sloughed, and the larva proceeds by an inch-worm motion. At the end of five days, larvae have been observed but little changed, the large pair of flame-cells easily visible. In two weeks the larva has elongated and appears as a sac-like structure within which developing daughter sporocysts may be seen. Measurements of ten specimens give an average of 0.85×0.19 mm. This stage is practically motionless except for a few periodical contractions. Each mother sporocyst gives rise to about twelve daughter sporocysts.

3. Daughter Sporocyst.

Daughter sporocysts emerge from mother sporocysts and actively migrate

to the edge of the gill. There they become attached by one end, the other elongating and projecting free into the mantle cavity. Ten specimens averaged 1.65×0.38 mm. This stage is fairly short and compact (Fig. 4), with each end somewhat constricted and apparently filled with refractile granules. The attachment end has an opening through which cercariae have been observed to crawl out. The wall of the sporocyst is fairly thick and irregular, with large cells scattered along its periphery. These cells may represent germ cells, as nowhere else were germinal elements encountered. Large flame cells, as described by Krull (1935), were often found, the arrangement of which, however, could not be determined. As many as ten cercariae have been found in one sporocyst, usually only 4-6. The bodies of the cercariae occupy the ends, while the whole central portion of the sporocyst is filled with the long, coiled tails.

4. Cercaria.

The cystocercous cercaria of *Gorgoderina attenuata* (Fig. 5) resembles very closely that of *Gorgoderina amplicava*. In fact, on first discovery, it was tentatively identified as *G. amplicava*. Further study, however, and the fact that no specimen of adult *G. amplicava* has been encountered, has shown the form here to be distinct from this other species. Total length varies from 8.753 to 9.628 mm.; anterior chamber, 0.363×0.264 mm., somewhat wider than anterior end of tail proper, bluntly oval, with an elongated anterior opening. Chamber itself (Fig. 6) hollow and contains cercaria body; apparently with no prominent structures. A pyramidal mass of granular cells, as observed by Krull (1935), arises from the base at junction with the tail stem. Although no attachment was found to exist between the cercaria and this mass of cells, this latter might be used as a support for the cercaria body. Tail proper cylindrical, tapering from a width anteriorly almost equal to that of the head chamber, to a bluntly rounded posterior end; transparent and structureless except for a few striae and nuclei more or less concentrated near the wider anterior end.

Cercaria body (Fig. 7) elongate oval, 0.409 mm. extended length, 0.264 mm. contracted; 0.118 mm. extended width, 0.165 mm. contracted; very active within head chamber. Cuticle covered with fine longitudinal striations. Sensory tubercles located on body: 14 on each side; 4 around anterior tip; about 40 around oral sucker; no sensory hairs of any kind, as recorded by Krull (1935), were identified.

Anterior tip of oral sucker and body prolonged to receive stylet. Stylet (Fig. 8) 0.035×0.008 mm., quite similar to that of *G. amplicava*; short point anteriorly, rounded posteriorly; two lateral wings arise at base of ventral surface of point and extend to posterior tip; fairly prominent median ventral keel present. Oral sucker $0.079 - 0.086 \times 0.071 - 0.074$ mm., with slight anterior projection to enclose stylet. Acetabulum somewhat behind body middle, $0.092 - 0.096 \times 0.081 - 0.089$ mm. Six pairs of penetration glands, distinct, between oral sucker and acetabulum; ducts convoluted and empty by six openings on each side of stylet at anterior edge of oral sucker (Fig. 7); cells granular with clear nucleus.

Mouth subterminal, opening directly into fairly long esophagus; esophagus bifurcates about halfway between oral sucker and acetabulum into two long, slender intestinal caeca which extend to posterior tip of body. Excretory pore at posterior tip, leading into long narrow bladder that extends almost to acetabulum; two lateral stems given off from bladder just below its anterior termination; each lateral stem divides into anterior and posterior collecting tubules that extend to each body extremity. Whole excretory bladder surrounded by large, closely packed, granular glands similar to those figured for *G. amplicava* (Krull, 1935). Genital anlage represented by a small mass of darkly-staining cells just posterior to acetabulum; a thin thread of similar material extends dorsal to acetabulum to its anterior edge, with a small concentration of cells at that point indicating the future genital pore.

Both living and preserved material were used in making this description. The genital anlage could be observed only in stained specimens and the penetration gland showed up distinctly with neutral red. Because of the highly refractile material of which the cercaria body consists, it was impossible to make out the complete pattern, even in immature specimens. A large, bluntly oval and transparent area across the esophagus and below the oral sucker represents the brain.

A study of developing cercariae in the sporocysts indicates that the tail is at first part of the cercaria body proper. With development, however, it apparently grows up around the body, detaches from the latter, and assumes the condition in the mature cercaria.

A comparison of the cercaria of *Gorgoderina attenuata* with other described cystocercous cercariae establishes its specific identity. It is much larger than those described by Wesenberg-Lund (1934), Krull (1935), or Miller (1936), nor does it have a shape comparable to the descriptions of many. It does resemble closely that of *Gorgoderia amplicava*, however, but may easily be distinguished by its large size, active body, and fewer cuticular tubercles.

5. Metacercaria.

Young metacercariae are very fragile and die almost as soon as they are ruptured from their cysts. Even older individuals are quite susceptible and perish under slight pressure. Cysts (Fig. 9) are quite characteristic and readily recognized under the dissecting microscope by their large size and by the opacity of their excretory bladder. Growth is rapid, a cyst of five days having a diameter of 0.138 mm., that of thirty-two days one of 0.510 mm. Cysts are infective from the start, since single-day infected tadpoles have been fed from which immature worms were later recovered. Cysts are not firmly attached to host tissue but lie free in the body cavity. They can be observed through the transparent abdominal wall of the tadpole to surge back and forth with body movement. Only when many cysts are close together do they seem to clump and stick together. No cyst wall of host origin has been definitely ascertained. The stylet is free in the cyst cavity almost immediately after the cyst wall is formed and may be found there throughout the life of the metacercaria. The larva is in constant motion, the anterior end probing from side to side within the cyst wall.

Removed from the cyst wall (Fig. 10), the metacercaria is much like the cercaria in shape. The number of tubercles is diminished to only four on each side and four around the stylet; only traces of those around the oral sucker may be found. A space for the stylet is still present as a small protuberance of the oral sucker and anterior end. An eight weeks metacercaria measured 1.32×0.363 mm.; oral sucker, 0.132 mm. and acetabulum, 0.264 mm. in diameter; esophagus shorter than in cercaria, which places intestinal fork much further anteriorly; caeca thick and extend to posterior end of body; bladder dilated to large sac-like structure between caeca; cystogenous glands around cercarial bladder disappeared; bladder filled with rosette-shaped refractive granules which may have resulted from breakdown of cystogenous glands; remains of penetration glands still visible between oral sucker and intestinal fork; anlage of genitalia somewhat more advanced: anterior to acetabulum the string of cells has advanced to the intestinal fork and expanded to form a large, solid structure with an indication of the genital pore; posteriorly, the rudiment of the vitellaria may be recognized, and directly below it, the developing ovary; vasa efferentia may be discerned leading from three primordial testes on one side and from six on the other.

6. Development of Adult Fluke.

Worms mature rapidly after introduction into the final host. An immature specimen (Fig. 11) in the intestine of an experimentally-infected newt showed the following characteristic: remains of the stylet cavity and penetration glands; vitellaria becoming characteristically dumbbell-shaped, ovary larger; testes fusing to two on one side and to four on the other; bladder empty. As specimens further down the intestine or up the ureters are examined, a whole series may be found demonstrating the fusion of testes to two. The three testes on one side become the anterior testis, and the six on the other, the posterior testis. Up to early immature adult stages, *Gorgoderina attenuata* is very similar morphologically to *Gorgoderina amplicava*. From there on, however, divergence to assume generic characters of *Gorgoderina* are observed. Such similarity in their life cycles is evidence of the very close relationship of these two genera and indicate a recent common ancestor. The adult worm (Fig. 12) has been well described by Stafford (1902) and Cort (1912) and will not be included here. It may be mentioned, however, that traces of testicular fusion may be discerned in the lobing of the immature and also adult testes.

Discussion

The several experiments reported here show quite conclusively that in the life cycle of *Gorgoderina attenuata* Stafford, 1902, the following hosts harbor the respective stages: *Sphaerium occidentale*, tadpoles of several species of *Rana* and larvae of *Triturus*, and adult *Rana* sp. and *Triturus*. It has been observed, also, that in attempting to infect various other intermediate hosts only *Pseudosuccinea columella* became positive, and this only occasionally. These observations indicate that tadpoles are the normal hosts for metacercariae of the genus *Gorgoderina*, whereas insect larvae and bivalve molluscs are normal hosts for metacercariae of the genus *Gorgoderina* (Sinitzin, 1905;

Krull, 1933, 1935; etc.). Lutz (1926) reported species of *Gorgoderina* encysting in the esophagus of dragonfly larvae. From his discussion, however, it is difficult to determine whether he was dealing with *Gorgoder* or *Gorgoderina*, since he refers indiscriminately first to one and then to the other. The results of the present study would indicate that he was using members of the genus *Gorgoder*.

Sphaerium in small containers with large numbers of miracidia often die, whereas controls and clams with but few miracidia survive. The miracidium, therefore, may be considered a contributing factor in the death of these animals. In nature, however, such confined conditions are not usually present, so that miracidia are probably not to be considered as an important limiting factor in the natural life of these molluscs.

Metacercariae excyst in the stomach of the tadpole, work their way down to the cloaca and then may be found in the ureters and kidney where they undergo further development. That this is not absolutely necessary is evidenced by the fact that immature individuals have been found in the bladder, while mature worms, containing ripe eggs, were in the kidneys of the same host. Odlaug (1937) also records the presence of a mature *G. attenuata* in the kidney. He found large numbers of immature *Gorgoder* *amplivava* in the kidneys and suggests that these may have been overlooked by Krull (1935) who indicated that about 80% of the metacercariae fed to a frog could not be accounted for. Odlaug's work and the present results would suggest that these two genera normally pass part of their life in the kidneys and assume later an adult habit in the bladder. As Odlaug points out, the presence of sexually mature *Gorgoderina capensis* in the abdominal muscles of *Rana esculenta*, reported by Joyeux and Baer (1934), is difficult to explain. Examination of many frogs from the area studied in the present work has revealed a fairly frequent occurrence of *Gorgoderina* cysts in abdominal muscles, many of which were precociously developed. Although no sexually mature individuals were found, still such a condition might possibly arise. In such cases, excystment with resulting migration might occur. On the other hand (Odlaug), abnormal physiological conditions might be responsible for such migration.

A study of the cercaria of *Gorgoderina attenuata* reveals certain difficulties in the system of classification of this group. Wesenberg-Lund (1934) includes *Gorgoder* and *Gorgoderina* in the *Macroceraria* of Luhe, distinguishing them from each other as follows: "In the *Gorgoder* group the anterior chamber occupies not more than $\frac{1}{6}$, commonly not more than $\frac{1}{10}$ of the total length of the tail. In the *Gorgoderina* group, it occupies about $\frac{1}{3}$." Certainly this grouping falls down when considering North American forms. As already pointed out, the cercaria of *Gorgoderina attenuata* resembles closely that of *Gorgoder* *amplivava*, especially with respect to ratio of chamber to total length. No specimens with short tails as figured by Wesenberg-Lund (1934) have been found, and Krull's (1935) description would indicate that the above grouping is not a natural one. Since these genera seem to agree so closely morphologically, the grouping under *Gorgoderinae* Cercariae, as suggested by Miller (1936) is maintained.

The genera *Gorgoderina* and *Gorgoderina* are apparently very closely related, not only morphologically, but also with respect to their life cycles and modes of development. The similarity of the different stages has been indicated. In *Gorgoderina* there is present at first 9 testes. Such a stage is comparable to the normal condition in sexually mature *Gorgoderina*. Later, these 9 testes coalesce to 2. The life cycle, then, may be used as another criterion to definitely separate these two groups of worms generically.

Summary

The life cycle of *Gorgoderina attenuata* Stafford, 1902, is described and figured. Adult flukes live in the bladder of various species of *Rana* and in *Triturus v. viridescens*. Miracidia hatch in the water, are swept through the incurent syphon of *Sphaerium occidentale*, and penetrate the gills to develop into mother sporocysts. A single generation of daughter sporocysts give rise to large cystocercous cercariae which are liberated into the water. Tadpoles pick up these cercariae along with algae, organic debris, etc. Cercariae penetrate the intestinal wall of the tadpole and form cysts throughout the body cavity, particularly around the heart and liver. Excystment occurs below the stomach of the definitive host when the tadpole is eaten. Developmental stages occur throughout the intestine and in the ureters and kidneys of the final host. This passage of part of the life cycle in the host's kidneys is believed to be normal. Metacercariae have nine testes; immature individuals show the gradual fusion to two as found in the adult worm. Such a condition indicates the close relationship to *Gorgoderina*, a bladder fluke with nine testes in the adult condition. A discussion of the literature and infection experiments is included. The significance of the life cycle as a means of establishing relationships is also discussed.

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AMHERST COLLEGE,
AMHERST, MASS.

DESCRIPTION OF FIGURES

All drawings made from experimentally-produced specimens, drawn with the aid of the camera lucida; all measurements in millimeters.



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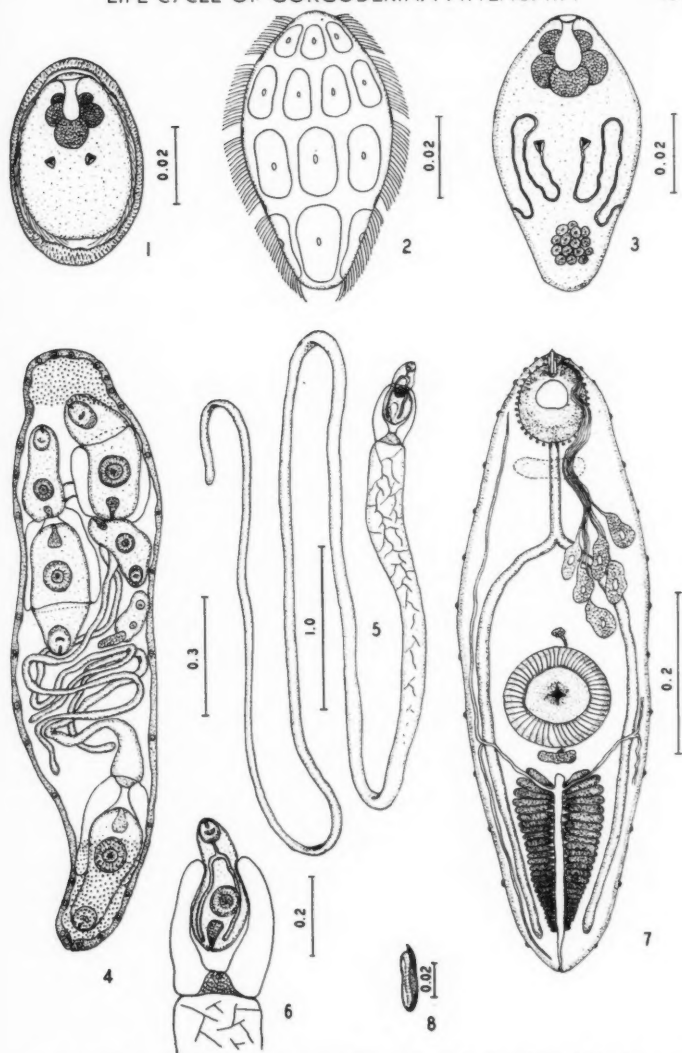


PLATE 1: Fig. 1, Egg with ripe miracidium, showing flame cells and glands around gut; Fig. 2, Miracidium with epithelial plates and cilia; Fig. 3, Miracidium showing excretory system and genital primordia; Fig. 4, Daughter sporocyst with developing cercariae; Fig. 5, Cercaria, entire specimen; Fig. 6, Enlargement of head chamber with body of cercaria; Fig. 7, Enlargement of body of cercaria to show body details; Fig. 8, Stylet.

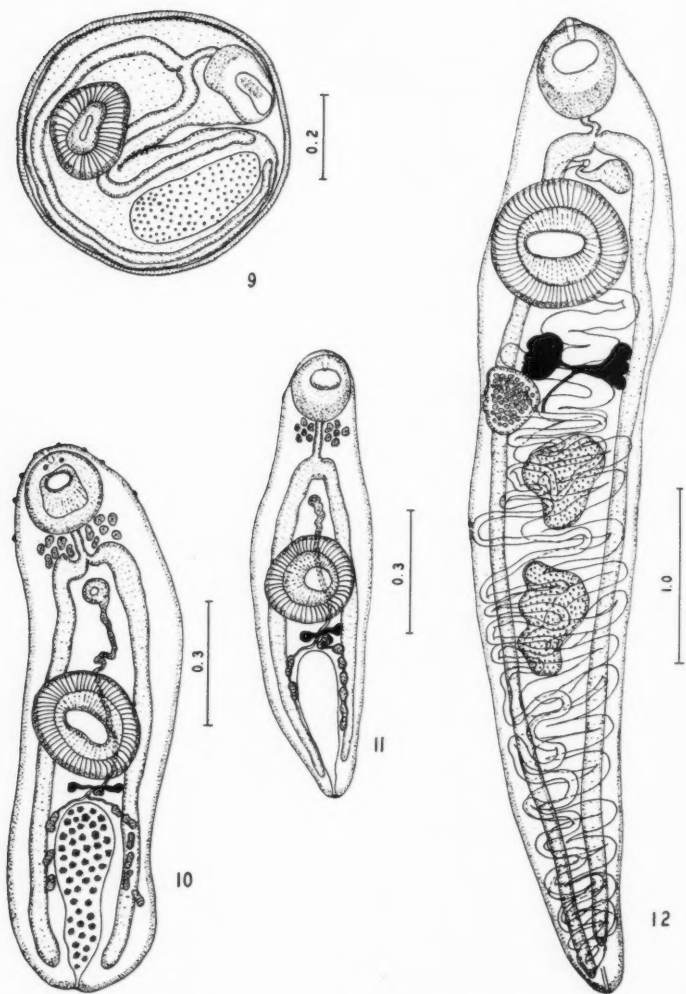


PLATE 2: Fig. 9, Metacercaria within cyst; Fig. 10, Ventral view of metacercaria removed from cyst; Fig. 11, Ventral view of immature adult worm from intestine of newt, note fusion of testes; Fig. 12, Ventral view of young adult worm from bladder of newt.

The Natural History of the Blind Goby, *Typhlogobius californiensis* Steindachner

G. E. MacGinitie

Introduction and History

That blind fish live in caves and in the depths of the ocean is a fact well known to biologists, but few biologists know that a blind goby, *Typhlogobius californiensis*, lives in the intertidal region along the coast of Southern California and Lower California. Its present known range is Point Vincente (north) to Ceros Island (south) (Barnhart, 1936). This goby has lived so long in a burrow under the rocks with *Callianassa affinis* Holmes, a shrimp (Pl. 2, Fig. 8), that, like many other fish living in similar circumstances, it is, in the adult stages, both blind and pink, having lost eyes and pigment. Over 200 individuals of this species that I have collected ranged between 20 and 80 mm. in length. The general form of their body reminds one somewhat of catfish, as it is rather heavy and blunt, particularly in the older specimens. The fin equipment resembles that of other members of the family Gobiidae, but is somewhat reduced. The pelvic fins are arranged in such a way that they constitute a sucking pad by which the fish can hold to any smooth object.

Typhlogobius californiensis was first named by Dr. Franz Steindachner in 1879, and was redescribed in 1881 as *Othonops eos* by Miss Rosa Smith, who later became Mrs. C. H. Eigenmann. Jordan and Gilbert (1882) included this fish in their synopsis of the fish of North America. In 1890 C. H. Eigenmann wrote an account of the fish and its relations in which he gives considerable detail of the skeleton and other morphological characteristics. In 1893 W. E. Ritter wrote an excellent account of the eyes, the integumentary sense papillae and the integument of this fish. Other than the original descriptions and the two morphological papers just cited, little has been written about this interesting goby. It is the purpose of this paper to describe the living animal and its life activities, and to include some notes on its embryological development.

What natural history notes are included in the papers just cited are, for the most part, incorrect. One fact, however, which was emphasized by these early authors is the extreme viability of this fish under artificial conditions. It will live for long periods of time in a small quantity of sea water and without food. This fact should make it of considerable value to physiologists, particularly those who would be interested in the conditions which make it possible for this fish to stand such extremes of oxygen depletion and pollution by its own excretions.

Habitat

*Typhlogobius californiensis*¹ lives commensally in pairs in the burrows of *Callianassa affinis*. These hosts also live in pairs and make their burrows in the sand along the beaches of Southern and Lower California where the rubble is sufficiently large to allow the deposition and holding of sand between and beneath the boulders. Pl. 1, Fig. 1 shows such a typical region. Because the shrimps feed by straining planktonic material from a current of water pumped through the burrow, it is necessary that there be more than two openings to this burrow and that the burrow be permanent. Therefore the burrows are built in those regions where the rocks of the beach are of sufficient size to prevent their being moved by tidal wash, and sufficiently numerous to hold the sand beneath them. The beaches of Southern California are, on the whole, fairly free from heavy surf, therefore the size of the rocks of the shingle may be smaller than would be necessary in more exposed regions. Where most of the rocks of the shingle are a foot or more in diameter, the required conditions are found.

Ritter (1893) was surprised that this goby did not inhabit the burrows of the "same shrimp" in the estuaries. However, in 1900 Holmes described the *Callianassa* with which *Typhlogobius* lives as another species, thus separating it from *Callianassa californiensis*, which is the estuarine species. I have verified this separation in two earlier papers by comparing the natural histories of these two shrimps (MacGinitie, 1934, 1937). The natural history of *Callianassa californiensis*, which inhabits the estuaries, is widely different from that of *Callianassa affinis*, the one with which the blind goby lives. It would be impossible for the blind goby to live in the burrows of *Callianassa californiensis*, for the latter does not maintain permanent burrows. Since the separation of the two species was made seven years after the publication of Dr. Ritter's paper, it is not surprising that Dr. Ritter considered the two shrimps of the same species, for, though their natural histories are so greatly different, it requires close observation to distinguish between the two species by means of their structural differences. *Typhlogobius* is quite specific in its choice of a host, as it has never been found in any burrows except those of *Callianassa affinis*. The burrows of this shrimp are confined almost entirely to the intertidal region, so that some of them at least are exposed at any stage of low water. It is my belief that during spring tides practically all their burrows are exposed.

Unless it be *Lethops connectens* Hubbs (1926), no other goby is known to remain permanently within the burrows of a host as does *Typhlogobius californiensis*. There is a certain amount of evidence which may throw some light on the evolutionary development of the strictly commensal condition exhib-

¹ There is only one species of this genus known. Hubbs (1926) has described another genus of blind goby, *Lethops connectens*, but practically nothing is known of this fish as only three specimens have been taken. I am inclined to think that it will be found more abundantly as a commensal in some burrow in the rocky regions beginning at about the lowest tides.

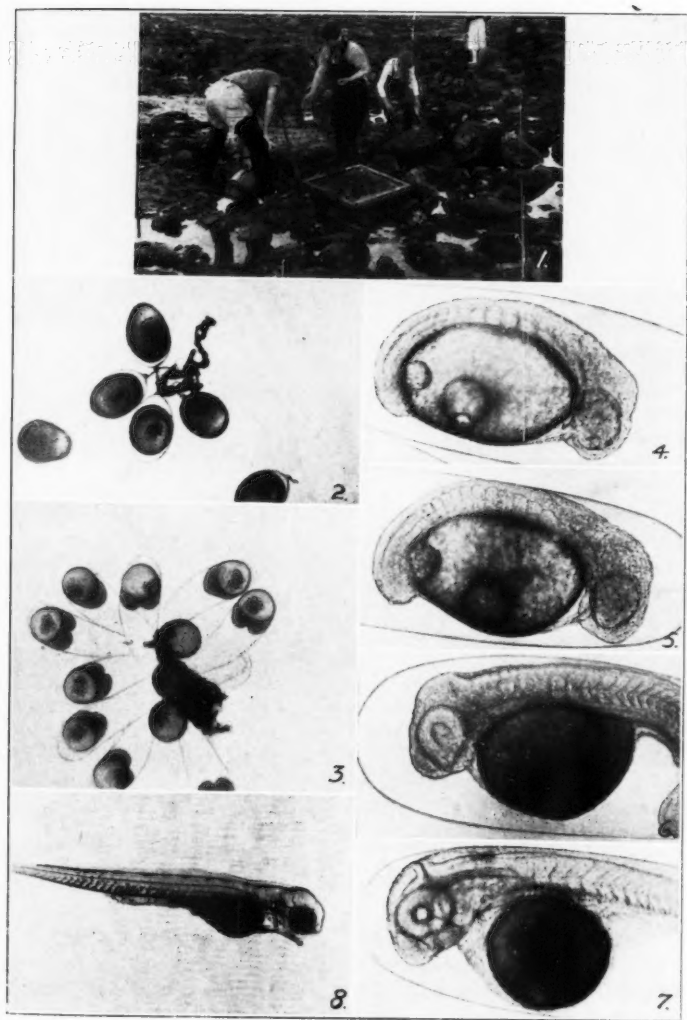


PLATE 1: Fig. 1—Collecting *Typhlogobius californiensis*; Fig. 2, Eggs taken just after being laid. Three fertilized, one not. x9; Fig. 3, First division. x6.8; Figs. 4-7, Successive stages in development. x34; Fig. 8, Newly hatched fish. x16.

ited by *Typhlogobius*. *Clevelandia ios*, the tiny goby mentioned by Ritter (1893) as living in certain burrows, has been found to use such burrows only as a place of refuge either from predators or during tidal exposure (MacGinitie, 1935). By watching the reactions of such animals as *Urechis* (Fisher and MacGinitie, 1928), *Callinassa californiensis* (MacGinitie, 1934), *Upogebia* (MacGinitie, 1930), etc. it becomes evident that the entrance of *Clevelandia* into their burrows is an invasion to which they are accustomed, for it does not disturb them, but they do become agitated when their burrows are invaded by animals other than *Clevelandia* or their typical commensals. *Gillichthys mirabilis*, another goby, may remain for a considerable period of time within the burrows of an animal such as *Upogebia*. Its eyes are somewhat reduced in comparison with those of *Clevelandia*, and it naturally seeks darker regions. It is but another step to the condition exemplified by *Typhlogobius*, where the fish remains permanently in the burrow of a particular host. Though the blind gobies may be derived, as stated by Hubbs (1927), from ancestors who lived beyond the tidal limits, I am of the opinion that the commensal habit has developed along the lines suggested above, and that either *Clevelandia* or *Gillichthys* could, in time, become commensal blind gobies. As will be explained later, I do not believe that a blind goby could persist as a species as a free-living animal, i.e., in rock crevices.

The burrows in which these gobies live are constructed entirely by the shrimps. They are rather tortuous, as they must follow to some extent the contours of the overlying rock, but they are not so extensive as those of *Upogebia*, another shrimp which also lives in pairs in a permanent burrow (MacGinitie, 1930, 1935). The pair of gobies remain in the deeper portions of the burrow, and exhibit very little activity except during periods of incubation of their eggs. It may be due to their habit of staying in the deeper portions of the burrow of the shrimps which gives them their great tolerance for stagnant conditions. *Hypsoblennius gentilis*, an estuarine blenny, will die within an hour in water in which *Typhlogobius* may live for months. *Typhlogobius* respire almost entirely through its integument, and it is mainly the rich anastomosing condition of the blood vessels near the surface which gives the fish its decided pink color. Apparently it is only during periods of vigorous activity or for a short time thereafter, that this fish makes use of its gills and operculi.

It might seem that the gills and operculi should show degeneration along with the eyes, but the fish use their operculi for creating food ingesting currents (that is, to suck food into the mouth), their gills for accessory respiratory organs, and their mouths and teeth for ingesting food and for fighting.

The death of both members of the pair of shrimps would result in the death of the gobies within a short time, as the fish are unable to keep the burrow in a state of usability, and, even if they were, they would starve in time, as they are unable to maintain a current through the burrow, which is necessary for bringing in food. Though, as has been stated before, the gobies will on occasion attempt to repel the invasion of other burrowing animals which may encroach upon their tunnels, they are not sufficiently aggressive to

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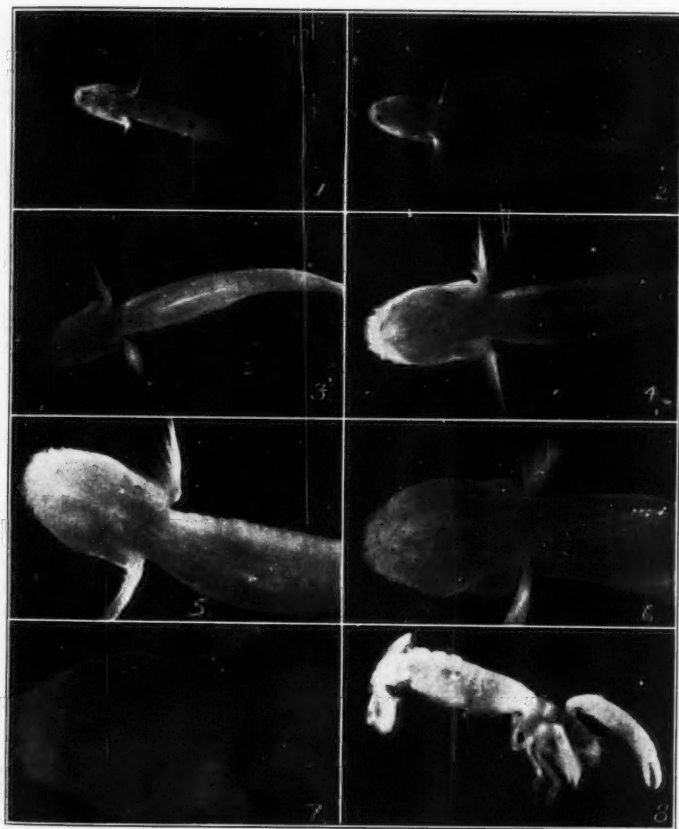


PLATE 2: Figs. 1-7, *Typhlogobius californiensis* ranging in length from 23 mm. to 85 mm. Note that in No. 6, although the fish is larger than No. 5, the eye spots are more conspicuous. In No. 7 no eye spots were visible under the binoculars. It will be seen that pigment also disappears No. 6 had been exposed to light for a considerable length of time, which causes more pigment to form than is usually present. x1.5; Fig. 8, the host, *Callinassa affinis*. x3/5.

meet with much success in keeping out other animals. It is their hosts which are ever on the alert to repel such invasions.

If it were not for the conditions found in the home of the host, a blind fish, such as *Typhlogobius californiensis*, would soon fall prey to such predators as the moray eel *Gymnothorax mordax* (MacGinitie, 1938), or the pistol shrimp *Crangon dentipes* (MacGinitie, 1937). There would be no constricted entrance to a rock crevice as there is to a burrow of *Callianassa affinis*, or, if a few such crevices could be found they would not be numerous enough to allow *Typhlogobius californiensis* to persist as a species. The fish would be devoured before they were large enough that the constriction of the rock crevice would form a protection. For these reasons I believe that the eyes of *Typhlogobius* were not lost in a darkened rock crevice, but after the goby became commensal with *Callianassa affinis*.

Feeding

The shrimp with which *Typhlogobius* lives obtains its food by straining microscopic material from a current of water which is caused to flow through the burrow by the action of swimmerets on the under side of the body of the shrimp. These paddles can create a fairly strong current and, since both the male and female shrimp may be feeding at the same time, it is necessary for the burrow to have a third or fourth opening. Coming in with this current of water are many small pieces of seaweed and other debris which may contain small animals or portions of animal flesh, the latter being derived mostly from the activities of predacious feeders on the surface, such as crabs when they tear their prey or carrion to pieces to enable them to eat it. This larger material is not ingested by the shrimp, but is allowed to fall to the deeper parts of the burrow where the edible portions are sorted out and eaten by the fish. Many times in the laboratory I have seen the *Callianassa* actually carry the larger material in its basket to the fishes and dump it before them.

Cooperation of this type among marine animals is not uncommon. Where animals are closely associated for great periods of time it is quite logical to expect that instinctive reactions to each other have evolved just as they have to other factors of their environment. Many fishes will carry portions of food too large to swallow to a crab or shrimp to be torn apart, and then they will dart in to take small pieces during the process. I have seen *Clevelandia ios* and *Leptocottus armatus* do this many times, and have also seen it happen in tide pools when some cottoids carried to a nearby crab a piece of mussel that I had fed them. The cooperation between commensal and host and between paired animals is but the manifestation of instincts developed in response to environmental factors.

The clearing from the burrow of many of the larger particles of food is, so far as I have been able to determine, the only possible benefit that *Callianassa* may derive from the presence of the blind gobies, that is, the fish by their omnivorous habits clean up most of the material which enters the burrow and is not used as food by the shrimp. Although this factor is more impor-

tant than one would at first assume, it is, however, of relatively small significance in that these materials could be carried to an entrance and forced outside just as is done with other foreign material which is rejected by the fish as food. But, even as it is, the shrimps spend a great deal of their time in activities which have to do with cleaning out the burrow, keeping it in shape, smoothing the sides and turn-arounds, and making repairs.

Because the blind fish live on finely divided seaweed and what suitable animal matter may enter the burrow, one of the best sources of food for specimens kept in the laboratory is the fore-gut of the sea urchin freshly taken from under water where it has been feeding. The sea urchin lives mainly on bits of seaweed which it chops into small particles by its teeth, and these particles are just the right size for feeding the fish, and, together with pieces of intestine, form a balanced diet for *Typhlogobius*. In the laboratory, however, I have made use of many sources of food, such as finely chopped dried abalone, gonads of many marine animals, crustacean larvae, bits of clam and fish, chopped seaweed, etc.

Sensory Responses

The data which furnishes the conclusions stated under this heading were gathered almost entirely during five years of observation in the laboratory. I establish a "family group" in the laboratory in the following manner:

A pair of shrimps are allowed to make a burrow, and when this is sufficiently extensive a pair of blind fish are placed on top of the mud. They wriggle their way down through one of the openings and make their way into the burrow with the shrimps. These burrows are made within a container which I have often referred to as a "limorium" (MacGinitie, 1935). A limorium consists of a frame in the sides of which are placed two glass plates, separated from each other at varying distances, depending upon the animals to be kept in it. The space between is filled with a combination of sand and mud, the consistency of which must be such that the burrows will not cave. For the *Callianassa* and its commensal blind goby, the sides of the limorium are separated about three-fourths of an inch from each other. Thus the burrow can be confined within a rather narrow space, and, though the burrow is not visible throughout all of its length, there are sufficient portions of it which come in contact with the glass on one side or the other that, after a period of several years of observations, one becomes quite certain that the activities of both the host and commensal are known.

The blind fish may also be kept in pairs in compartments of an aquarium without their hosts and without any possible contact except with the glass sides of the aquarium and its contained sea water. I have kept many pairs of fish in this manner for several years. They will, however, make use of a glass tube under such conditions, particularly during periods of inactivity, but they leave and enter such tubes at will.

There seems to be no sensory relationship between the goby and its host except one of passive tolerance. The callianassas get along just as well with-

out the fish in the burrow. As before mentioned, the callianassas will carry food to the fish if the latter are present, or the shrimps will also push one or both of the fish out of the way as they pass along the burrow, or will even sometimes pinch them with the large claw to make them move. These reactions to the presence of the fish are the only ones I have ever seen exhibited by the shrimps. On the other hand, except when they are brooding their eggs, the fish are entirely indifferent to the callianassas.

The fish meet their environment almost entirely through chemotropic and thigmotropic responses. The keenest sense which they possess is chemotropic. In comparison with most free-living marine animals, the remainder of their senses are exceedingly dull, and, in comparison, even their senses of smell and of touch are considerably reduced. They can sense the presence of food in the runway or in the burrow, and will wriggle along in the direction from which the current is bringing them the scent, and then will locate the food by the tactile papillae situated around the mouth. They sort out the food material from the other debris by touching it with one or more of these sensory papillae. Of course, they can, and sometimes do, reject particles after they have been taken into the mouth. Though these tactile papillae (see Ritter, 1893) are undoubtedly developed to perform a tactile function, they are not nearly so sensitive as, for example, the tips of the arms of an octopus or the hairs on the dactyls of most crabs and shrimps. However, under the conditions in which the fish live, particularly because of the lack of competition, the papillae are sufficiently sensitive for their needs.

As is also the case with their hosts, the gobies become quite concerned about the presence of other animals within the burrow, even of annelid worms over two inches in length. Worms smaller than this they will eat, but, though the fish have a fairly capacious mouth, it seems impossible for them to swallow objects much larger than an eighth of an inch in diameter. Since the entrances of the burrows are constricted to a considerable extent, being usually no larger than from 2 to 5 mm. in diameter, few invaders ever enter the burrow, and if they do the Callianassas usually eject them, though the fish will sometimes fight such invaders. More will be said about the tactile and olfactory senses of these fish under Mating or Pairing, and Reproductive Activities.

The eyes of the newly hatched *Typhlogobius* are perfectly normal, but after the fish take up their abode in the burrow of a pair of shrimps, the retina withdraws to some extent, usually becomes twisted out of shape, and covered with body layers until in most adults the eyes are indiscernible (see Ritter, 1893). There is, however, some variation in the visibility to the observer of the eyes in fishes of the same size. But, so far as I have been able to determine, any goby of whatever age or size is able to distinguish between strong light and darkness, though this reaction becomes less marked as the fish grows older and the eyes become more deeply covered by the body layers. At all times the fish exhibit a tendency to remain deep within the burrows, that is, they seek that portion of the burrow which is deep and level. Since this reaction is carried out in total darkness, it is impossible to say whether the presence of a strong light also causes them to make this reaction. But in

any case, it is evident that a strong light will agitate a blind goby of whatever size or age.

The blind gobies are more concerned about their tactile adjustments than they are about being in the dark. They are, of course, also sensitive to vibrations in the water. As is the case with most fishes, *Typhlogobius* will head into a current of water, though not with the determination that many fish exhibit. The *Callianassas* with which the blind gobies live will soon die if not kept in a tube or burrow where they can come in contact with its walls. This is not true, however, of the fish, though they do exhibit some tendency to remain in the angle of the sides of an aquarium, or, as has been mentioned before, will spend more time within a glass tube if one is present than would be true if they were making only a hit or miss adjustment.

No stimulus other than forcible ejection will cause a blind goby to leave its burrow, but, like *Urechis* (Fisher and MacGinitie, 1928), if a chemical sufficiently strong be introduced, it will die in the burrow instead of leaving. However, I have never tried poisoning tidepools. Since they are so securely hidden in the burrows of the shrimps, these fish, when once established, are practically free from the attacks of enemies. I have never seen any indication of the burrows of the shrimp host having been dug out by any predacious feeder. In the first place, the burrows are too extensive for a predator to obtain sufficient returns for his efforts. The predator would have to be small, as the burrows often penetrate crevices between the rocks which are no larger than the burrow of the shrimp. Considering these things, I know of no predator of the right size which is equipped for such activity. Enemies are shown to be practically non-existent by the fact that both the fish and their hosts have a relatively long life span. This conclusion is the result of the following data: 1. Careful screening shows few juvenile shrimps and fish in comparison with the number of adults. 2. Fish which have been kept in the laboratory for as long as four years, and well supplied with food, grow slowly. One pair which I had had in the laboratory for four years has grown from about 75 mm. to 82 mm. in this length of time. This pair is now the largest of this species of fish that I have seen. From the amount of growth shown by other smaller blind gobies that I have had in the laboratory, I suspect that these were at least six or eight years old when they were brought in, so that a conservative estimate would place their age now at not less than ten or eleven years.

These fish are extremely hardy and are able to undergo adverse conditions which would be fatal to any other tidepool fish with which I am acquainted. As long as their skin is kept moist with ocean water they will continue to live for a period of a week or more. Also, if put in a jar of sea water they may be kept there at least two or three weeks without any change. They may be handled a great deal without any apparent ill effect, and, though their skin seems to be soft and tender, it is exceedingly tough.

In summing up the tropisms of the blind goby it can be said that all senses are somewhat degenerate, and that this fish would be unable to live even underground in a burrow without the ministrations of its host. The advantage, therefore, is all on the part of the blind goby. It is not necessary

for a state of commensalism to begin as a symbiotic relationship. In a case such as the one herein being described the relationship was commensal from the beginning.

Mating or Pairing

Typhlogobius mates early and remains paired throughout life. Pairs of *Typhlogobius* with an over-all length of less than 20 mm. have been taken from burrows on the beach. Since the newly hatched fish is 3.25 mm. in length, and the egg-laying season is during the two months from the middle of May to the middle of July (mainly in June), and since these paired fish were taken in December, it means that pairing takes place sometime within the first six months of the life of the fish. The fish become sexually mature the first summer after hatching, that is, in one year. Pairing, therefore, occurs before sexual maturity, i.e., the first spawning. The life span is not known, but, from all indications, it can easily be 10 or 15 years, and apparently parallels that of the host.

Small gobies are nearly always found with small callianassas, though this does not always hold strictly true. However, never have I found a very small pair of fish with large callianassas, and, from what has been said, it is evident that the opposite would be impossible. Usually the callianassas and the blind fish are of about the same size. The life history of the goby after hatching and up to the time pairing takes place, that is, the first four months of its life, is still unknown. It is hoped that within the next two or three years this portion of the life cycle will be solved. The gonads begin to develop when the fish is about six months of age, and constantly enlarge until the following summer. From this time on the fish show a very strong fighting instinct toward others of their own sex, and this accounts for the fact that never are more than a pair of blind gobies found in any one burrow. For instance, if a male goby invades the burrow of an established pair, the two males will at once enter into combat and continue until one or the other is killed or driven from the burrow. During this time the female is indifferent to what is going on, unless, as will be shown later, it is during the period of the incubation of the eggs. The same thing is true if another female enters the burrow, for then the two females will fight until one or the other is destroyed or driven out. The fish are equipped with a good set of small, sharp, needle-like teeth. In fighting, one fish will bite the other and hang on, sometime for two or three hours. If the attacked fish is able it will twist its body and also take a good hold on its adversary. At intervals after this, one or both fish perform shaking movements which apparently serve only to set the teeth deeper in the wound. Fighting of this type, in which the fish maintain their biting hold for such long periods of time, could be engaged in only by fish which respire mainly through the integument, as it is impossible for any water to pass over the gills while the fish has its mouth full of its adversary. If one fish bites the other near the head in such a manner that the fish which is bitten cannot at the same time obtain a hold on its adversary, it in turn takes the next bite, for evidently the jaws of the first attacker eventually tire sufficiently that the fish which is held can finally wriggle loose. I once saw two of these fish

remain attached to each other for several hours, one having hold of the lower jaw of the other, while its own upper jaw was in turn firmly held in the mouth of the other. Upon the release of one fish by the other a crescentic set of bloodshot punctures will be left where the teeth of the biter have punctured the skin of the victim. This sort of fighting will continue for two or three days or until, as has been said before, one or the other is killed or forced out of the burrow—usually the former.

That these fish pair and that they engage in combat only with members of the same sex is sufficient evidence that they can distinguish sex by a chemotropic sense. However, certain other reactions of this fish verify this conclusion. If a blind goby inclosed in a thin cellophane tube closed at both ends is placed in a burrow with an established pair of blind gobies, no particular attention is paid the object by either member of the pair. If, however, a small opening is made in the cellophane, then the member of the pair which is of the same sex as the fish in the cellophane wrapper will become quite active and will begin searching for the invader. Too, if one handles a goby and then puts one's hand in an aquarium with an established pair of blind gobies, that individual of the pair which is of the same sex as the fish which was handled will often exhibit the fighting instinct, but for only a few minutes, as there is undoubtedly a complication of the human scent with that of the fish scent on the hand, the latter losing its strength very rapidly. That these gobies recognize the opposite sex by a chemotropic sense emphasizes the important biological principle of variation, for Breder (1935) found that with his guppies "sex recognition is feeble if present at all," and Noble (1934) found that sex recognition in the sunfish *Eupomotis gibbosus* depends mainly on form and movement, and (1938) that the females of the jewel fish *Hemichromis bimaculatus* "will select the most highly colored of several possible mates," while with the males "sex identification is a matter of learning." In fact, by comparing the guppy with the blind goby we have shown two extremes, one in which there is practically no sex recognition and the other in which sex recognition is not only very acute, but in which the fish pair permanently.

Though pairing takes place early, and, without disturbance, lasts through life, if an invader enters the burrow and kills its rival, the other member of the pair accepts its new mate without even any indication that the change has been made. These blind fish may be moved around and pairs broken up and exchanges made, but so long as only one male and one female remain together, there will be no fight. When, as is often the case, only single members of a pair are obtained from the tidepools when one is collecting, they can be paired in the laboratory by allowing eliminative combat, or by using an established pair in which one knows the sex of the individuals. In time one becomes able to distinguish between the sexes of the medium sized or larger individuals, particularly at the time the gonads become filled, as the ovaries and testes may be seen through the body wall, the former being yellow, and the latter cream colored. Too, at such times the female is considerably more robust than the male, and, in the larger, older fish, the female is always somewhat broader in the head and body than is the male.

By using an established pair in which the sex of the individuals is known the collected material may be separated into male and female by placing the gobies one at a time with the known pair and leaving them there only long enough to determine whether it is the male or the female that becomes concerned. In using this method it is well to allow 10 or 15 minutes to elapse between the introduction of each fish to be tested. For example, if a male has just been placed with the established pair and taken out and another fish, say a female, is immediately introduced, the male may attack it, because of the fighting instinct having been stimulated by the male which had just previously been introduced. By careful collecting, however, one is usually able to obtain both members of a pair in the field and to keep them together for establishment in the laboratory.

Egg Laying Activities

The sex products develop in the gonads of *Typhlogobius* for several months before egg laying takes place. The amount of sex products developed depends upon both the size of the gobies and the amount of food available. Along the coast of Southern California it frequently happens that the plankton and debris are pretty meager during the fall and well into the winter months, so that it can be said that in general the eggs and sperm which are mature at laying time (which has its peak about June) began their development about the first of February. Through observations of the spawning seasons of many of the marine animals over a period of thirteen years I have found that the spawning times may vary a great deal, depending upon such factors as food, temperature, etc. This holds true for these blind gobies, and it may even be that more than one spawning takes place in a season, that is, if a pair of gobies spawn in early May the chances are that they will spawn again in July. In the laboratory, due to the abundance of food and somewhat higher temperatures, three and four spawnings a year may be obtained from a pair of these gobies.

It is also possible to produce spawning in both sexes by injecting the fish with the hypophysis from another fish. For this purpose I use members of the genus *Paralabrax*, or, as they are commonly called, kelp bass or sand bass, because they can be caught from the front porch of the laboratory. However, I suppose that the hypophysis of any other common fish would work as well. The hypophysis is mascerated with a pestle in a mortar with a little seawater, and is then injected under the skin of the blind goby with a hypodermic needle, $\frac{1}{4}$ cc. of a fairly concentrated solution being sufficient. One may expect the injected fish to spawn within less than a month. It is, of course, necessary that the fish be well supplied with food during this time. By this means I have obtained as many as 6 or 8 spawnings in a year from one pair of fish.

One group of blind gobies that I collected and did not separate into pairs seemed to get along very well together for several days, as is usual. This group was then injected with hypophysis and still left together. Fighting began during the third night after the injection, and the following morning several of the fish were dead and others were still engaged in a battle to the

finish. Under such conditions any male or female will take a biting hold on any other fish of the same sex, and thus there may be three or four in a group which are attached to each other by their jaws. Of course, since there was no control group, it is impossible to say whether or not the injection of hypophysis caused the fishes to begin fighting sooner than they otherwise would. However, blind gobies which are allowed to remain in a group after being collected do not usually begin fighting until they become more accustomed to their new surroundings, which requires more time than in the above instance.

By actual count the eggs laid and fertilized in one spawning by a pair of blind gobies somewhat above average size totaled $11,000 \pm 50$, all of which hatched. By fairly close estimates the spawnings of others have ranged between 2500 and 15,000 eggs, depending upon the size of the pair.

Egg-laying is always preceded by certain definite activities on the part of gobies. The first indication of the approaching spawning is a tendency of the two fish to remain more of the time in bodily contact, and often as they are thus in contact shivering or shimmying movements pass along the body of first one and then the other of the fish. This may continue for several days or a week, and then the two fish will begin to clean a space on the glass of the aquarium or the side of the burrow where a rock or shell affords a smooth surface. The pelvic fins are well forward just beneath and posterior to the pectoral fins and are fused together to form a sucker-like cup of the type found on the common tidepool (clinging) fish *Caularchus maeandricus*, though the sucker on the under side of the goby is not nearly so large, fleshy and strong as it is on *Caularchus*. During the cleaning process the gobies, first one and then the other of the pair, attach themselves here and there by means of this cup, and, by wriggling their body, clean the surface by rubbing it with the ventral side of the body, the pectoral fins and the anal fin. During this cleaning operation the fish may remove projections or sessile objects by means of their mouths. Under natural conditions, in the burrow with its sandy walls, some excavating may be done. I have seen only the male engaged in this latter activity, but it is possible that the female may help also. It is impossible, of course, to see within a burrow, but on two occasions the egg laying was done so that it could be seen through the opening of the burrow in a limorium. In one case the eggs were laid on the glass of the limorium, and in the other upon a shell. In these two cases the male made available a larger surface for the attachment of the eggs by removing some of the sand. The sand is moved by fanning it loose with the pectoral fins, by carrying it in the mouth or by a combination of both methods. The goby deposits the sand in the runway, from where the shrimps either carry it to another portion of the burrow and smooth it out, or carry it to the entrance and push it outside.

Occasionally during periods of rest from their cleaning activities, shimmying movement are indulged in. At the end of about two days of cleaning preparation, egg laying begins. The female extrudes an almost transparent ovipositor about $\frac{1}{4}$ inch long and begins to deposit eggs at the rate of 1.4 eggs per second. The deposition of each egg is accompanied by a movement

of the posterior portion of the body of the female to one side and downward, she at the same time clinging to the surface of the rock or glass by the sucker already described. As each egg is laid a little forward movement takes place so that the eggs finally come to be scattered about over the surface prepared. After depositing eggs for a period of two or three minutes (average), which means somewhere between one and two hundred eggs, the female moves away and the male moves over the eggs and at the same time gives off sperm to fertilize them. The time that the female spends in laying before moving away and allowing the male to fertilize the eggs varies a great deal. Occasional turns have been as long as 5 or 6 minutes for the female, though the time spent by the male over the eggs is much more uniform, and, I think, never more than two minutes. The first eggs laid are deposited singly, but later eggs are placed both adjacent to and attached to the stalks of the first ones laid until the whole becomes a plate, the eggs of which are segregated in bunches somewhat resembling grapes.

When the eggs are first laid the case ranges from 675 to 720 microns wide and 780 to 870 microns long, and the egg practically fills the case (Pl. 1, Fig. 2). Immediately after the egg is fertilized the case or membrane begins to elongate, and attains a length of from 2700 to 2850 microns. The shape of the case to some extent anticipates the shape of the future embryo (Pl. 1, Fig. 3). One laying of 5,040 eggs was laid between 2:25 p.m. and 4:45 p.m., making a total of 2 hours and 20 minutes for the entire laying. The first division occurs about 2 hours, or a little more, after fertilization. In the case of the laying just cited, the first division took place 2 hours and 15 minutes after fertilization. The second division, which is at right angles to the first, occurred at 5:50 p.m., or 1 hour and 10 minutes after the first. To develop from the 2-cell to the 4-cell stage requires about 40 minutes, from the 4-cell to the 8-cell stage about 40 minutes, and from the 8-cell to the 16-cell stage about 35 minutes.

The embryo fish surrounds the yolk at about 17 to 18 hours, and at about the beginning of the fifth day it extends beyond the yolk and reaches the end of the capsule. From this time on the tail must be turned back along the side of the body, and after this occurs the tail is reversed from side to side occasionally. Pigment in the eyes and along the head and back begins to form about the end of the fifth day. Fins are formed about the seventh day. (See Pl. 1, Figs. 4-7.)

The incubation period is between 10 and 12 days, and during this time both the male and the female are very attentive to the care of the eggs. At intervals one or the other, or sometimes both together, will pass over the eggs and fan them with their pectoral fins, thus keeping the eggs clean. On the day that the fish hatch both gobies are busy, constantly working at the eggs, and the movements of the bodies of the parents over the eggs seem to facilitate the escape of the embryos from the egg cases. As soon as the last eggs hatch the parent fish lose all interest in the empty egg cases.

This cleaning of the eggs is not uncommon among those marine animals which have a fairly long incubation period and which attach their eggs in some

way. In addition to certain fishes, octopi and many crustacea display this cleaning activity to a high degree (MacGinitie, 1934). When this cleaning activity is not kept up the eggs of some fishes, crustacea and octopi will become so overgrown with detritus and fungus growth that the embryos will die before hatching.

As stated above the eggs of the blind goby hatch in about 10 to 12 days at temperatures ranging from 17 to 20° C. At the time of hatching the eyes of the fish are perfectly normal and they have a considerable amount of pigment scattered over the dorsal side (Pl. 2, Fig. 8). Those hatching in the light show considerably more pigment than those which hatch in the dark. The larval fish wriggle out from the large end of the capsule, and, at the time of hatching they still carry a considerable amount of yolk, which disappears about three days later. Colored blood cells make their appearance 4 days after the fish have hatched, or shortly after the yolk has been absorbed. The larvae are positively phototropic from the time they hatch, and continue thus for a week after hatching. I have never carried the fish to the stage where they become negatively phototropic and seek underground burrows.

During the time that the embryos are developing within the egg capsule the parent fish not only clean and care for the eggs, but will unitedly attempt to defend them against any intruders. During this time the male and female will engage in combat with fish of either sex. They also prevent the callianassas from coming in contact with the eggs, and will often bite at one's fingers or a glass tube. In other words, they resent the movement of any object near the eggs, particularly of any living animals other than their hosts, and, as has just been said, cannot be moved from their protective position even by the callianassas.

Blind fish will not eat their own young, at least not for many days after hatching, but blind gobies other than the parents will readily eat the newly hatched larvae.

Summary

1. The blind goby *Typhlogobius californiensis* lives commensally in the burrows of the shrimp *Callianassa affinis*. These burrows are intertidal along the coast of California and Lower California, and there are one pair of shrimps and one pair of blind fish in each burrow. The burrows are found only where the boulders of the rocky region are sufficiently large to allow the deposition and holding of sand between and beneath them.

2. A probable evolutionary sequence resulting in the lack of pigment and eyes of *Typhlogobius* is given.

3. The blind gobies are entirely dependent upon the activities of the shrimps for their persistence as a species.

4. The food of the gobies consists of either animal or plant detritus which find their way into the burrows with the currents created by the hosts. An excellent source of food in the laboratory is the gut of the sea urchin.

5. Chemotropic and thigmotropic senses are fairly well developed; the others are decidedly degenerate.

6. The eyes and pigmentation are normal in the newly hatched *Typhlogobius*, but both begin to disappear after the fish take up their abode in the burrow of a pair of shrimps.

7. When once established underground the fish have no enemies. The fish and their hosts have a life span of at least 10 or 12 years.

8. These blind fish pair early and remain paired throughout life. Their spawning season is from May until July, mainly during June.

9. The gobies are very sensitive to the invasion of other blind gobies of their own sex, i.e., a male will at once engage in mortal combat with an invading male, and a female will do likewise with an invading female. One of a pair will accept a new mate at any time.

10. The recognition of the sex of the invader is entirely chemotropic.

11. The spawning activities consist of cleaning a space for the deposition of the eggs, the laying of the eggs by the female and their fertilization by the male. This is followed by the concerted efforts of the pair to guard the eggs and to keep them clean until they hatch about 10 days later.

12. It seems fairly certain that the injection of a pair of blind gobies with the hypophysis from a marine bony fish induces spawning out of season. The estimated number of eggs in spawning in the laboratory ranged between 2500 and 15,000.

13. Embryological development follows the normal course exhibited by other members of the family.

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Four New Rabbits from the Upper Pliocene of Kansas¹

Claude W. Hibbard

During the summer of 1937, the Kansas University Museum of Vertebrate Paleontology continued its Field Work on the Upper Pliocene Fauna of Kansas. With the cooperation of Messrs. Joe Tihe, Harry Jacob, Ben Bagrowski, Fred Holden, and Vernon Carter, students of the University, a large collection of vertebrates was obtained from the Upper Pliocene. Four apparently new rabbits were collected, which are described in the following paper. Since the work has not been completed in this area, the discussion of the fauna as a unit and its relationship to other faunas will appear at a later date.

I wish to thank L. R. Dice for numerous helpful criticisms and suggestions during the course of this study.

The drawings were made by Walter Yost of the University of Kansas.

Subfamily *Palaeolaginae* Dice

Pratilepus gen. nov.

Genotype.—*Pratilepus kansasensis* sp. nov., No. 4582, Kansas University Museum of Vertebrate Paleontology; incomplete right ramus with P_3 , P_4 , M_1 and M_2 .

Diagnosis.— P_3 triangular in outline, with base at posterior border of tooth, two external reentrant angles. The posterior external reentrant angle narrow and crenulated on posterior border, extending over halfway across crown of tooth. Anterior external reentrant angle well developed, nearly as long as the posterior external reentrant angle, extending nearly halfway across the anterior portion of the tooth, posterior enamel border slightly wavy. Two internal reentrant angles, the anterior very shallow, containing cement, the posterior deeper, extending one-fourth the distance across the crown of the tooth. P_4 , M_1 and M_2 with heavily crenulated reentrant angles extending across the crown. P_2 with three anterior reentrant angles. The lingual angle being shallow. The middle angle deep, extending more than halfway across crown of tooth. Labial angle slightly deeper than lingual. P_3 , P_4 , M_1 and M_2 with internal reentrant angles extending three-fourths of the way across the crowns of the teeth and heavily crenulated on the anterior borders, wavy on posterior borders, but with tendency for waviness to disappear in the posterior teeth. (*Pratilepus* from *pratun*, plain, and *lepus*, hare).

¹ The study involving the description of these species has been forwarded by a grant from the University of Kansas Graduate Research Fund.

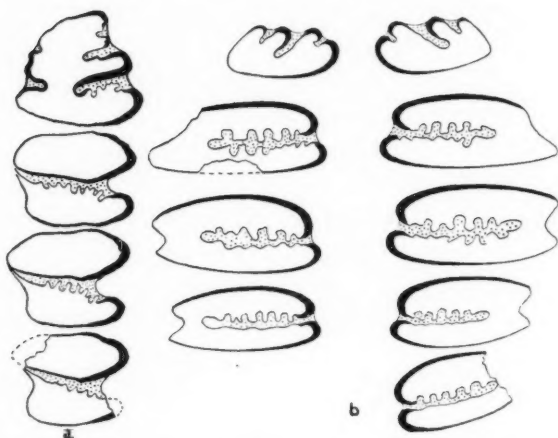


Fig. 1. *Pratilepus kansasensis* Hibbard, n. gen. and sp., (a) holotype, showing crown view of right P_3 , P_4 , M_1 and M_2 of K.U.M.V.P., No. 4582, $\times 6$; (b) showing crown view of right and left upper P_2 , P_3 , P_4 , M_1 and left M_2 of K.U.M.V.P., No. 4566, $\times 6$.

***Pratilepus kansasensis* sp. nov.**

Holotype.—No. 4582, Kansas University Museum of Vertebrate Paleontology; incomplete right ramus with P_3 , P_4 , M_1 and M_2 .

Paratypes.—Nos. 4574, incomplete right ramus with P_3 , P_4 , M_1 and M_2 ; 4575, part of left ramus with I, P_3 , P_4 , M_1 and M_2 ; 4579, incomplete right ramus with P_3 , P_4 and M_1 ; 4580, incomplete left ramus with P_3 , P_4 and M_1 ; 4581, incomplete left ramus with P_3 , P_4 and M_1 ; 4592, left ramus with I, P_3 , P_4 , M_1 , M_2 and M_3 ; 4566, upper maxillaries with P_2 , P_3 , P_4 , M_1 and M_2 .

Horizon and Type Locality.—Upper Pliocene, Meade County, Kansas, Locality No. 3, Rexford fauna.

Description of Type.—(See table of measurements). An incomplete right ramus bearing P_3 , P_4 , M_1 and M_2 , of a rabbit the size of *Sylvilagus audubonii neomexicanus* Nelson; length of tooth row, 10.7 mm. P_3 contains two external reentrant angles and two internal reentrant angles. The anterior external reentrant angle is well developed, extending 1.2 mm. across the anterior part of the tooth which is nearly halfway across the anterior part of the crown. The angle is filled with cement. The posterior external reentrant angle is well developed, extending slightly over halfway across the crown of the tooth; it is filled with cement and the posterior enamel border is crenulated. The minor anterior internal reentrant angle is opposite the anterior

external reëtrant angle. It is a slight indentation in the outer wall of the enamel extending to the base of the tooth filled with cement. The posterior internal reëtrant angle is well developed extending at least one-fourth the way across the crown of the tooth and to the base of the tooth; it is also filled with cement. The greatest anteroposterior diameter of P_3 , 3 mm.; greatest transverse diameter, 3 mm. P_4 , greatest anteroposterior diameter, 2.2 mm.; greatest transverse diameter, 3.1 mm. The greatest anteroposterior diameter and the greatest transverse diameter of M_1 and M_2 are the same as P_4 . The molariform teeth have heavily crenulated reëtrant angles extending across the crown of the tooth. The mental foramen is small, about one-half the size of the foramen of *Sylvilagus audubonii neomexicanus* and located slightly nearer P_3 . The jaw is heavier than that of *S. a. neomexicanus*.

Description of Paratypes.—Paratypes No. 4574, 4580, 4581 agree with the type in dentition pattern. No. 4579 is a younger individual in which the posterior internal reëtrant angle is well developed and nearly meets the posterior external reëtrant angle. They are separated by a very small bridge of dentine. Nos. 4592 and 4575 are dentitions of old individuals which are more greatly worn. In these the posterior internal reëtrant angle exists only as a well developed enamel island, without connection to the outside, but not separated by a tract of dentine. In both cases the anterior enamel border of the island is much heavier than the posterior. In specimens 4579 and 4592 the anterior part of the angular process is present. The angular process is more posterior in position to the dental series than in *S. a. neomexicanus*. In *Pratilepus kansasensis* its attachment is posterior to M_3 . M_3 of *Pratilepus kansasensis* is composed of an anterior oval column completely separated from the posterior column by a band of cement. The posterior column is not as terete as that of *S. a. neomexicanus*. No. 4566 consists of the maxillaries and palatine bridge. Right M^2 and M^3 , and left M^3 are missing. P^2 has three anterior reëtrant angles. The median angle extends over halfway across the crown. The lingual angle is well developed but extends the shortest distance across the crown. The labial angle is as wide as the median angle and extends twice as far across the crown of the tooth, as does the lingual angle. The labial side of P^2 is not as angular as that of *Sylvilagus a. neomexicanus*. The anterior border of the palatine bridge is opposite the posterior border of P^2 . The posterior border of the palatine bridge is opposite the posterior border of P^4 . The opening of the external nares is as wide as that in *S. a. neomexicanus*. The internal reëtrant angle of the molariform teeth is heavily crenulated and extends nearly as far across the crown of the tooth as in *S. a. neomexicanus* but the difference is too slight for measurement. The upper dentition of *Pratilepus kansasensis* has a slightly greater transverse width than that of *S. a. neomexicanus*.

Discussion.—The figures of *Alilepus annectens* (Schlosser) are so poor that it is impossible to work out the true relationship of that genus with *Pratilepus kansasensis*. *Pratilepus kansasensis* represents a more advanced form of the *Palaeolaginae* due to the development of the anterior external reëtrant angle, the heavily crenulated external reëtrant angles of the lower molariform

teeth and the well developed anterior reentrant angles of P^2 . The relationship of *Alilepus? vagus* Gazin, is uncertain, due to inadequate material. The anterior external reentrant angle of *Alilepus? vagus* is much shallower than that found in any of the old worn dentitions of *Pratilepus kansansensis*. In fact, in the worn dentition, that angle is not found to be reduced in the material at hand, though the anterior internal reentrant angle may be completely missing. *Pratilepus kansansensis* is distinguished from *Pliolagus beremendensis* Kormos by its retention of the posterior internal reentrant angle in old worn teeth, also by the heavily crenulated reentrant angles of the lower molariform teeth.

Table of Measurements of *Pratilepus kansansensis* (In millimeters)

	Type						
	4582	4574	4580	4579	4575	4592	4581
Depth of mandible below M_1 measured on inner side.....			13.3	13.3	13.4	13.	
Thickness of mandible below M_1	4.4		4.45	4.7	4.6	4.6	
Length of diastema between I and P_3						14.9	
Length of tooth series							
P_3 - M_2 inclusive.....	10.7	10.5			10.5	10.6	
I anteroposterior diameter.....						1.9	
I transverse diameter.....						2.3	
P_3 greatest anteroposterior diameter.....	3.	3.	2.8		3.15	2.9	2.9
P_3 greatest transverse diameter.....	3.	2.9	2.6		3.	2.5	2.8

Dicea gen. nov.

Genotype.—*Dicea lepuscula* sp. nov., No. 4583, Kansas University Museum of Vertebrate Paleontology; right ramus bearing incisor, P_3 , P_4 , M_1 , M_2 and M_3 .

Diagnosis.— P_3 with large median crenulated internal reentrant angle reaching more than halfway across the crown of the tooth. No anterior reentrant angles; posterior external reentrant angle not crenulated and reaching halfway



Fig. 2. *Dicea lepuscula* Hibbard, n. gen. and sp., holotype, showing crown view of right P_3 , P_4 , M_1 , M_2 and M_3 of K.U.M.V.P., No. 4583, x6.

across crown of tooth. Anterior external reentrant angle only slightly developed, a broad flat rectangular groove is present. The enamel of the exterior reentrant angles of the molariform teeth not crenulated. Mental foramen large. This genus is named for Dr. Lee R. Dice, who has devoted much time to the study of the fossil *Lagomorpha*.

Dicea lepuscula sp. nov.

Holotype.—No. 4583, Kansas University Museum of Vertebrate Paleontology; right ramus bearing incisor, P_3 , P_4 , M_1 , M_2 and M_3 .

Paratype.—No. 4584, K.U.M.V.P.; fragment of left ramus bearing P_4 , M_1 , M_2 and M_3 .

Horizon and Type Locality.—Upper Pliocene, Meade County, Kansas, Locality No. 3, Rexford fauna.

Description of Type.—A small rabbit about the size of *Hypolagus? apacheensis* Gazin. Right ramus bearing incisor, P_3 , P_4 , M_1 , M_2 and M_3 . The incisor has a transverse diameter of 1.9 mm. and an anteroposterior diameter of 1.5 mm. The incisor is separated from P_3 by a diastema of 11.7 mm. The diastemal region of the ramus is slightly lower than the alveolar border of P_3 and extends anteriorly with a very slight downward slope. Since the incisor is not as strongly curved as in other rabbits it gives the diastemal region a nearly horizontal appearance. The mental foramen is twice as large as that of *Sylvilagus floridanus alacer* and is situated close to the anterior external base of P_3 . The length of the tooth series P_3 to M_3 inclusive, measured at the occlusal surface is 9.3 mm. P_3 is nearly rectangular in shape, with a slightly narrowed anterior portion. P_3 has a well developed median internal reentrant angle, with deep crenulations in the enamel, extending more than halfway across the crown. The internal reentrant angle is situated anteriorly to the apex of the enamel on the inner surface of the tooth, and lies between the two external angles. No reentrant angle or angles are present on the anterior face of the tooth. The anterior external reentrant angle is actually a broad nearly flat groove, deepest at its anterior and posterior borders. The posterior external reentrant angle is well developed and extends halfway across the crown of the tooth. The posterior enamel border has no crenulations. It is separated from the posterior deflection of the internal reentrant angle only by a narrow tract of dentine. The internal and external reentrant angles all contain cement. The external reentrant angles of P_4 , M_1 and M_2 extend completely across the crowns of the teeth and are filled with cement. The enamel borders are not crenulated. M_3 consists of two oval columns separated by a band of cement. The posterior part of this tooth is two-thirds the size of the anterior. (Lat., *lepuscular*, a little hare).

The paratype agrees with the type, but unfortunately lacks P_3 . The depth of the mandible below M_1 , measured on the inner side, is 11.4 mm. The length of the P_4 to M_3 inclusive, measured along the occlusal surface, is 8.4 mm. The posterior part of M_3 is smaller than in the type.

Subfamily *Archaeolaginae* Dice

Hypolagus regalis sp. nov.

Holotype.—No. 4572, Kansas University Museum of Vertebrate Paleontology; incomplete left ramus bearing incisor, P_3 , P_4 , M_1 and M_2 .

Paratypes.—No. 4571, K.U.M.V.P. incomplete right ramus bearing P_3 to M_2 inclusive; and No. 4567, K.U.M.V.P. incomplete left ramus bearing P_4 to M_3 inclusive.

Horizon and Type Locality.—Upper Pliocene, Meade County, Kansas; Locality No. 3, Rexford fauna.

Diagnosis.—Largest of the known species of *Hypolagus* represented by lower dentition. The anterior external reëtrant angle of P_3 wide, enamel slightly crenulated and extending nearly halfway across the tooth. The posterior external reëtrant angle narrow, with slightly crenulated enamel, angle extending slightly more than two-thirds of the distance across the tooth.

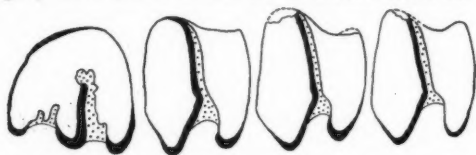


Fig. 3. *Hypolagus regalis* Hibbard, n. sp., holotype, showing crown view of left P_3 , P_4 , M_1 and M_2 of K.U.M.V.P., No. 4572, x6.

Description of Type.—Incomplete left ramus bearing incisor, P_3 , P_4 , M_1 and M_2 . Length of tooth series at alveolar border, 12.8 mm. The incisor is well developed, extending posteriorly to the anterior border of P_3 , but shifted lingually so as to produce a marked thickening of the jaw at its termination. The incisor has an anteroposterior diameter of 2.3 mm. and a transverse diameter of 2.8 mm. A diastema of 17 mm. separates the incisor and P_3 . P_3 is strongly cylindrical in outline along the anterior, lingual and labial surfaces. The posterior surface is slightly flattened. The anteroposterior diameter of the tooth is 3.2 mm. and equals the transverse diameter. Two reëtrant angles are present on the labial surface. The anterior external reëtrant angle is wide and extends nearly halfway across the tooth. The enamel is slightly crenulated possessing a well developed loop. The posterior external reëtrant angle is narrow and extends slightly over two-thirds of the distance across the tooth. Its enamel along the posterior border is slightly crenulated throughout its length by a series of shallow waves. The angles are well filled with cement. P_4 , M_1 and M_2 with well developed external reëtrant angles extending across the crowns of the teeth to the enamel. The enamel of the reëtrant angles shows no tendency toward crenulation; they are well filled with cement. The mental foramen is well developed and larger than that of *Lepus townsendii campanius*. The foramen is also situated closer to the anterior border of P_3 . The length of the dental series corresponds more nearly to that of *Lepus americanus americanus* but the mandible is decidedly heavier. (Lat., *regalis*, of a king, alluding to size plus Rexroad fauna).

The paratypes agree with the type. M_3 of No. 4567 agrees well with the M_3 of *Lepus* excepting that the posterior portion is not as terete and is more angular.

Hypolagus regalis is larger than the other known species of Upper Pliocene *Hypolagus*. P_3 of *Hypolagus furlongi* Gazin from the Grandview, is more triangular in shape with a shallower anterior external reëtrant angle. *Hypolagus limnetus* Gazin from the Hagerman Lake Beds, is much smaller than *Hypolagus regalis*, though the anterior external reëtrant angle of the former seems to be as well developed as in the latter.

Subfamily indet.
Pediolagus gen. nov.

Genotype.—*Pediolagus progressus* sp. nov., No. 4570, Kansas University Museum of Vertebrate Paleontology, portion of right ramus bearing broken incisor, P_3 , P_4 and M_1 .

Diagnosis.— P_3 with anterior reentrant angles, and two external reentrant angles. The posterior external reentrant angle extending slightly over halfway across the crown of the tooth and crenulated on posterior border. Between the posterior external reentrant angle and the enamel of the lingual side of P_3 is a well developed enamel island filling with cement and separated from the lingual enamel border by a tract of dentine.

Pediolagus progressus sp. nov.

Holotype.—No. 4570, Kansas University Museum of Vertebrate Paleontology, portion of right ramus bearing broken incisor, P_3 , P_4 and M_1 .

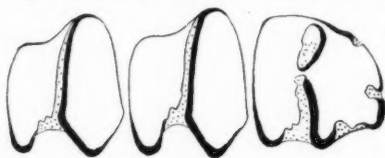


Fig. 4. *Pediolagus progressus* Hibbard, n. gen. and sp., holotype, showing crown view of right P_3 , P_4 and M_1 of K.U.M.V.P., No. 4570, x6.

Paratypes.—Nos. 4568, portion of right ramus bearing P_3 , P_4 and M_1 ; and 4569, the anterior portion of the left ramus with incisor and P_3 .

Horizon and Type Locality.—Upper Pliocene, Meade County, Kansas, Locality No. 3, Rexroad fauna.

Description of Type.—Portion of right ramus bearing broken incisor, P_3 , P_4 and M_1 . Length of tooth series, 10.4 mm. P_3 not as cylindrical as in *Hypolagus regalis*, the anterior part of the tooth is narrower, resembling more the P_3 of *Lepus* in outline. Anterior reentrant angle present. It is well developed, extending to base of tooth and filled with cement. The anterior external reentrant angle is wide, enamel slightly wavy. The posterior external reentrant angle is narrow and extends slightly over halfway across the tooth. The posterior border of the enamel of the reentrant angle is decidedly crenulated. Between the reentrant angle and the enamel of the lingual side of the tooth is a well developed enamel island filled with cement. The anterior border of the enamel island is heavier than the posterior border. The posterior border of the enamel of the island is finely crenulated. The antero-posterior diameter of P_3 is 3.3 mm.; the transverse diameter is 3.2 mm. The external reentrant angles of P_4 and M_1 extend completely across the crowns of the teeth and are well filled with cement. The posterior enamel borders of the reentrant angles of these teeth are not crenulated. Mental foramen greatly

reduced, as small as that of *Lepus americanus americanus*. (Pediolagus: $\pi\epsilon\delta\iota\omicron\nu$, plain; $\lambda\alpha\gamma\omega\varsigma$, hare, in allusion to the type locality).

The paratypes agree with the type. P_3 of No. 4568 has two well developed anterior reentrant angles, the most exterior being the larger, both are well filled with cement. The posterior external reentrant angle extends half-way across the tooth. The enamel island is well developed. The anterior enamel border of the island is heavier than the posterior enamel border, which is crenulated.

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MUSEUM OF VERTEBRATE PALEONTOLOGY,
UNIVERSITY OF KANSAS,
LAWRENCE, KANSAS.

Central Wisconsin Muskrat Study

F. N. Hamerstrom, Jr. and James Blake

Central Wisconsin is a typical example of footless drainage in the Lake States. Once with more marsh than dry land, the country was ditched about twenty-five years ago in an ill-starred agricultural venture. The marshes were drained and duly planted to crops but the expected profits—except to the land speculators—failed to materialize. Farms were abandoned one by one, fires ate out most of the peat, and the job was called a failure.

From the standpoint of the water-loving furbearers it was more than a failure; it was a disaster. With the marshes and swamps gone, the streams straightened, most of the stream bottom woods cut out, they had only the ditches to turn to. The federal government bought 100,000 acres of this wasteland in 1935 to make the Central Wisconsin Game Project, Necedah.* Two hundred miles of man-made ditch, sometimes wet and sometimes dry, was almost the only remaining habitat for muskrat, beaver, otter, and mink on this area.

Project development plans include fur management. In 1936 and 1937 we studied the furbearers, using repeated surveys over the whole ditch systems as our study method. Five surveys were run, in two springs, two summers, and one autumn; fur sign was recorded in maps and notes. The survey technique, summary of findings for the major species, and a more detailed description of the area, have already been reported (Hamerstrom and Blake, 1939).

The present muskrat situation on the Project is a matter of more than local application. It is directly comparable with conditions on many of the drained areas throughout the Lake States, and probably in much of the rest of the Middle West as well.

The best muskrat water was in the rather shallow open ditches in the "high marsh" country—alternating shallow peat, black (Dunning) sand, and scattered islands of white (Plainfield) sand. Here the ditches follow in a general way the old marsh basins, occasionally cutting through low sand islands and ridges. As a result, high marsh ditch bottoms are made up of sand, muck, and some shallow peat, offering a variety of growing conditions. Water varies from slightly acid to slightly alkaline; plants and animals with high calcium requirements, such as musk grass (*Chara* spp.) and clams do not occur. Even in mid-summer the coldness of the water is remarkable. The spoil banks are mainly sand and are grazed very lightly or not at all.

Well-shaded ditches, and those which were deep and swift through most of the year, were practically barren of muskrats. Such ditches had very little food in the water or on the banks.

* Project LD-WI-5, Farm Security Administration, Region II; Mr. W. T. Cox, Regional Forester-Biologist.

A review of the seasonal cycle clearly shows the weakness of the drainage ditch environment: spring dispersal of a small breeding nucleus over a greatly expanded range; in summer the range drying up, population on the move but making a strong recovery none the less; by late autumn muskrats many and well distributed; winter decimation. Unstable water levels and shortage of winter food combine to cut the value of the ditch range to a fraction of its potential.

WATER

Water levels were constantly varying. In spring, melting snow and ice and rains filled most of the ditches to the berm level. At that season the muskrat range was at its maximum; except for the swift-running main ditches, the bottoms of which were scoured clean by the rush of water, suitable territories were many and well distributed, greatly exceeding the numbers of animals present. From the spring high the water rapidly dropped lower and lower, rising temporarily after each heavy storm. By early summer much of the potential muskrat range was dry or nearly so, and it continued to shrink until autumn. Autumn rains partly re-filled the ditches. Through the winter, however, these gains were lost, as the water drained away faster than it was replenished. Many ditches froze to the bottom before spring.

Ditch heads and short laterals were the preferred breeding grounds in spring. As the season advanced the water in these places dwindled to small pot-holes, drying up one by one. Their bottoms generally remained wet enough to grow quantities of young grasses and spike rush (*Eleocharis* spp.), good food, but the muskrats had followed the water down the ditch. Like Errington's (1937) muskrats, once our muskrats had chosen winter territories they showed a strong tendency to stick out in spite of later food or water shortages; during late spring and summer, perhaps because of breeding activities, they were much less tolerant of such changes. A constantly shifting population—and this during the breeding season—was the result. In both years shifting was pronounced, many cases exactly paralleling one another.

A few fairly stable breeding areas were provided by such favorable spots as beaver ponds, deep holes in bends or behind drift jams, and some of the deeper main ditches (avoided earlier). Errington (1937) noted a similar reliance on scattered nuclei in Iowa drainage ditches.

FOOD HABITS

Food habits were studied by collecting plant fragments in feeding platforms, noting cuttings and diggings, and watching feeding animals whenever possible. We are particularly indebted to Dr. N. C. Fassett, Curator of the Herbarium of the University of Wisconsin, for help in identifying the small bits of plants taken from the feeding platforms.

The food list, except for a long list of miscellaneous plants which appeared only once or twice, is given in Table 1.* We found no animal foods.

* Since both Latin and common names are given in the table, common names only are used in the text.

TABLE 1. Food Plants

Latin name	Common name	Part used	Winter	Spring	Summer	Autumn
<i>Acorus Calamus</i>	Sweet flag	Lower stems	†	ss	ss	†
<i>Anacharis (Elodea) canadensis</i>	Water-weed	Stems & leaves	ss	ss	ss	ss
<i>Asclepias incarnata</i>	Marsh milkweed	Roots	ss	ss	ss	ss
<i>Calla palustris</i>	Marsh calla	Roots	ss	ss	ss	ss
<i>Calamagrostis</i> sp.	Bluejoint	Roots & lower stems	ss	ss	ss	ss
<i>Carex</i> sp.	Sedge	Roots & sprouts	††	ss	ss	ss
<i>Carex Crawfordii</i>	Sedge	Culms	ss	ss	ss	ss
<i>Carex crinita</i>	"Wideleaf"	Roots & sprouts	†	†	†	†
<i>Carex rostrata</i>	"Wideleaf"	Roots & sprouts	†	†	†	†
<i>Carex stricta</i>	Wire grass	Roots & sprouts	ss	ss	ss	ss
<i>Cirsium</i> sp.	Thistle	Stems	ss	ss	ss	ss
<i>Cyperus strigosus</i> (?)	Galingale	Culms	ss	ss	ss	ss
<i>Dulichium arundinaceum</i>		Stems	ss	ss	ss	ss
<i>Eleocharis</i> sp.	Spike rush	Roots	††	ss	ss	ss
<i>Eleocharis acicularis</i>	Spike rush	Roots	††††	ss	ss	ss
<i>Eleocharis obtusa</i>	Spike rush	Roots	ss	ss	ss	ss
<i>Erigeron canadensis</i>	Mare's tail	Stems	ss	ss	ss	ss
<i>Eupatorium perfoliatum</i>	Boneset	Stems	ss	ss	ss	ss
<i>Galium</i> sp.	Bedstraw		ss	ss	ss	ss
<i>Glyceria</i> sp.	Manna grass	Culms	ss	†	†	†
<i>Graminae (unidentified)</i>	Grasses	Culms	ss	†	†	†
<i>Hypericum</i> sp.(prob. <i>H. majus</i>)	St. John's-wort	Lower stems	ss	ss	ss	ss
<i>Iris virginica</i> var. <i>Shrevei</i>	Iris	Roots & lower stems	†	ss	ss	ss
<i>Juncus</i> sp.	Rush	Bases & roots	ss	ss	ss	ss
<i>Juncus effusus</i>	Rush	Bases & roots	ss	ss	ss	ss
<i>Leersia oryzoides</i>	Rice cut-grass	Roots	ss	ss	ss	ss
<i>Lycopus uniflorus</i>	Bugleweed	Tubers	†	†	†	†
<i>Ludvigia palustris</i>	Water purslane	Base of stalk	ss	ss	ss	ss
<i>Myriophyllum</i> sp.	Water milfoil	Stems & leaves	ss	ss	ss	ss
<i>Muhlenbergia</i> sp.		Culms	ss	ss	ss	ss
<i>Muhlenbergia foliosa</i>		Culms	ss	ss	ss	ss
<i>Najas flexilis</i>	Bushy pondweed	Stems & leaves	ss	ss	ss	ss
<i>Nymphaeanthus variegatus</i>	Spatterdock	Fruits & rootstocks	ss	ss	ss	ss
<i>Nymphaea alba</i>	White waterlily	Rootstock, bases of petioles	ss	ss	ss	ss
<i>Polygonum</i> sp.	Smartweed	Lower stems	ss	ss	ss	ss
<i>Populus tremuloides</i>	Aspen	Stems & bark	ss	ss	ss	ss
<i>Potamogeton</i> sp.	Pondweed	Lower stems	ss	ss	ss	ss
<i>Potamogeton ephedrus</i>	Pondweed	Lower stems	ss	ss	ss	ss
<i>Proserpinaca</i> sp.	Mermaid weed	Stems & leaves	ss	ss	ss	ss
<i>Quercus</i> sp.	Oak	Acorns	ss	ss	ss	ss
<i>Rubus</i> sp.	Dewberry	Roots	ss	ss	ss	ss
<i>Rubus</i> sp.	Raspberry	Roots	ss	ss	ss	ss
<i>Rumex</i> sp.	Dock	Base of stalk	ss	ss	ss	ss
<i>Sagittaria latifolia</i>	Arrow-weed	Base of stalk & root	ss	ss	ss	ss
<i>Salix</i> sp.	Willow	Bark	ss	ss	ss	ss
<i>Solidago</i> sp.	Goldenrod	Stems	ss	ss	ss	ss
<i>Sparganium americanum</i>	Bur-reed	Whole plant	ss	ss	ss	ss
<i>S. chlorocarpum</i>	Bur-reed	Whole plant	ss	ss	ss	ss
<i>Spiraea salicifolia</i> or <i>S. tomentosa</i>	Spiraea	Stems	ss	ss	ss	ss
<i>Typha latifolia</i>	Cat-tail	Roots	ss	ss	ss	ss
<i>Utricularia</i> sp.	Bladderwort	Stems & leaves	ss	ss	ss	ss

Key: †—Heavily utilized; ‡—Moderately utilized; §—Slightly utilized.

In comparison with the whole list, the winter dietary is marked by the fewness of the plants represented. Three species, *Carex crinita*, *C. rostrata*, and bugleweed, were of outstanding importance. The first two, known locally as "wideleaf," were the chief winter staples of the ditch muskrats. Roots and basal portions of the plants were eaten in quantity. Their staple quality was shown by their importance during winter and their diminished use in the seasons of wider choice. Cat-tail, a preferred food, was uncommon on the area; these two sedges were used as much in winter as cat-tail is in other places. Sweet flag was even less abundant than cat-tail, but was heavily used in late winter wherever available. Three square (*Scirpus americanus*), a major muskrat food in many localities, does not grow on the Project.

The third major winter food, tubers of bugleweed, was unique among the food plants in that it was eaten in great quantity at all seasons of the year. It was almost constantly present in the feeding platforms, and the spots at which muskrats had been digging for it were very conspicuous.

Moderately used winter foods include the roots of several other species of *Carex*, and spike rush. Less use was made of them during spring and autumn. Lower stems of iris were rather extensively taken where available, but did not bulk large in the total amount of food taken.

The winter staples, bugleweed, and iris were heavily fed upon in early spring, but were soon supplemented and largely replaced by other species. The new growth of grasses, for the most part not identified, was extensively cut, some probably for nest material. Manna grass was particularly heavily fed upon, *Muhlenbergia* occasionally. Shoots and lower stems of sedges, including the important wideleaf, were heavily represented. Bur-reed, as long as it remained available, was one of the most sought foods. Among the newly appearing plants, spatterdock, pondweed (chiefly *P. epiphydrus*, the most common species in the ditches), and dewberry shoots were moderately fed upon, and occasional use of practically every available plant became noticeable.

Because of the great abundance and diversity of available foods there seemed to be little need of a study of summer food habits. Few collections were made; hence the scantiness of the data in the table. Bugleweed, manna grass, pondweed, arrowweed, bur-reed, and goldenrod were conspicuously taken. In general, summer foods were much the same as spring foods, except that as the tender new growth became tougher and coarser with age, some of them were dropped from the list.

In autumn, a number of the most important summer foods—manna grass, pondweed, and bur-reed—continued to be important, and the winter staples again became prominent. Two foods of a single season importance appeared, St. John's-wort and acorns. In one ditch, the only place where it was found, bushy pondweed was a major food. Grasses, rushes, and spatterdock were moderately used, together with a fairly large list of miscellaneous material.

WINTER CRISIS

The foregoing data on food and water conditions set the stage for the winter drama.

In spite of unfavorable breeding conditions the population was able to build up to such a point that by the time the ditches were partially filled again by autumn rains, sign was abundant and well distributed over the Project. During the winter, however, the population suffered drastic losses.

In both years a very low spring population was found. Since the survey was not started until 1936 we did not have a comparable record of muskrat distribution during the preceding autumn. Local trappers, however, are agreed that the situation as described is typical of every year. In the autumn, cruising the ditches to canvass the fur crop, they find many rats: in spring, when trapping usually starts, only a fraction remain. Without denying the long-time muskrat cycle noted by Henderson (1923), it is plain that the 1936-37 die-off was not a cyclic drop, as the same thing happens year after year.

The following description of conditions on five ditches, arranged in the form of an H and totalling four and one-half miles in length, is illustrative of winter losses: During the first spring (1936) we found a light scattering of muskrat sign, the equivalent of slightly over a half-mile of sparsely occupied ditch. By autumn all five ditches had heavy sign along their full extent. Thick growth of bur-reed and pondweed provided an excellent autumn food supply, and the rats were in place a few days before freeze-up. The water supply was adequate through the winter by reason of a plug at the downstream ditch junction. On the spring survey of 1937 there was sign along less than half the total ditch length, and most of that was scattered. There were very few late winter feeding beds. The muskrats had not been trapped out.

Four and one-half miles are included in this illustration. To realize the loss over the whole Project, multiply by forty.

It may be argued that the decrease in muskrat density was the result of population movements: that the muskrats simply moved to another place. As is commonly the case, a few actually were found in spring in places which had had none the autumn before, but the general shrinkage of occupied territories so far outweighed these scattered gains as to make them insignificant.

It is highly probable that there was winter movement in search of food and water. Errington (unpub.), however, has shown that such winter wandering results in heavy losses through intraspecific strife, predation, hunger, and cold. Further, there was no marked increase in the river bottoms to the east and southeast nor in the cranberry reservoirs to the north and west, the only places to which muskrats leaving the Project could go with any chance of survival. Enders (1931) considers a dislike of burrowing in sand, because of caving in of sand burrows, an explanation of the absence of muskrats "from otherwise desirable places." It cannot be regarded as the explanation here. Sand or no sand, the muskrats had been there in the autumn, and sand burrows were commonly used.

The most probable cause of the winter decrease lies in an unbalance between food and water supplies. In the ditches cited as an example, the two main foods—bur-reed and pondweed—die back in the winter and do not have fleshy roots. Root foods were almost wholly lacking in the water and along the banks. Ice reached to the bottom during the winter. In varying measure the same situation or its opposite, food without water, applies to the whole Project. Such a condition, while it does not kill every wintering muskrat, unquestionably reduces carrying capacity to a fraction of its potential.

Water conservation is the most important step in correcting the present condition. Plantings might hasten the establishment of winter foods. From the survey maps the key points at which such work is most needed can readily be found; from the food habits data the important foods to be encouraged can be determined. Not so much *more* water as more constant levels at all seasons is needed; not so much *more* food as winter food of species known to thrive under the conditions found on the Project.

UNSOLVED PROBLEMS

Finally, two unsolved problems of some interest were encountered. Ditches through deep peat had almost no muskrats. It may be that lack of food is a limiting factor during winter, but spring and summer foods were more than adequate. Peat in itself can hardly be unattractive: witness the high productivity of the coastal marshes of Louisiana (Louisiana Department of Conservation, 1931) and Maryland (Bailey, 1937). On the Maryland marshes, indeed, Smith (1938) considers a peaty bottom one of three essentials for good productivity. We were unable to follow up the question, as the area on which the peat work was started was dropped from the Project and had to be dropped from our study. There are practically no ditches through deep peat on the Project.

Again, not all the breeding season shifts could be explained on the basis of food and water. In the presence of seemingly ideal conditions, sections of ditch as much as a quarter to a half mile in length were several times wholly abandoned. To solve these problems, like those of sex ratio, size and number of litters, effect of predation, called for a more detailed study than we were able to make.

One point, of late increasing in importance in muskrat ecology, has not been brought forward. Fur management is a part of the Project development plan. A high yield of muskrats is one of its objectives. What then of the cranberry growers on the edges of the area, who must constantly hold down the rats in their reservoirs, beds, and channels, or go out of business?

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DIVISION OF WILDLIFE MANAGEMENT,
UNIVERSITY OF WISCONSIN,
MADISON, WISCONSIN
AND
FARM SECURITY ADMINISTRATION,
NECEDAH, WISCONSIN.

Elisha Newton Plank

John T. Buchholz

Elisha Newton Plank was an active botanist and collector of southwestern plants during 1880-1900. He carried on his work independently without the advantages of school or college connections. The story of his life and activities have become a matter of increasing interest to systematic botanists. His better known botanical activities center in Kansas, Texas, and Arkansas, but we find that he came west from



Elisha Newton Plank, 1831-1907

New York and was of New England parentage. He was born March 23, 1831 near Wolcott,¹ Wayne County, New York, and died September 21, 1907 at Decatur, Arkansas.

The subject of this sketch was the youngest of several children, a descendant of New England families who had furnished soldiers to the Continental Army, and it is not surprising that at the outset of the Civil War we find that he organized a company of volunteers at Wolcott, of which he was chosen captain, but could not himself qualify for active service because of physical defects.

¹ Anonymous—History of Wayne County, New York. Page 207. Philadelphia, 1877.

Elisha Newton received his education in a private school at Wolcott, and entered Falley Seminary at Fulton, New York, in the autumn of 1853. Upon his return home from the seminary early in 1854, where he had given up his studies on account of ill health, we find from a journal which he had kept during this period (1853-55), that he seemed determined to make up for his loss of a formal college education and formed a habit of devoting some time daily to study. The entries in his diary are not merely trivial matters. They show reflective thinking and a genuine longing for knowledge. His essays and public addresses during this period afford delightful reading. He must have been a young man of unusual potentialities who became a self-educated gentleman of high attainments. Botany was always a favorite subject, undertaken at any convenient time, while the reading of Virgil, English literature, history and the works of philosophical writers usually occupied his evenings. This studious habit was kept up throughout his life. His private library contained the books valued by cultured men of his period. He also started a botanical garden in which he experimented in the cultivation of plants brought in from the woods and fields. In his marriage to Marsylvia Amelia McIntyre he found a companion who had also enjoyed educational advantages in seminaries and who shared his keen interest in plants. A local herbarium was begun, of which he wrote: "This is only the commencement of what, if I live, shall be an extensive collection of plants. I hope one day to be a botanist."

In the concluding pages of this journal, we find a list of scientific binomials and common names of more than three hundred of the native and naturalized species of the vicinity of Wolcott. This list demonstrates that Plank had a wide acquaintance with plants at an early period of his life, before he came west. He was thoroughly conversant with the technicalities of botanical descriptions and must have had his foundations in the subject before the appearance of Gray's *Lessons in Botany*. In this period Botany was not yet recognized as a subject suitable for colleges and schools.

In this journal there is mention of a local "Botanical Association" which had been in existence and of which he was the leader and teacher before his matriculation at Falley Seminary. This society was reorganized after his return and kept going for some time through the cooperative interests of him and his wife, held weekly meetings and conducted excursions to the local regions of botanical interest. We also find mention of the "Lyceum" or literary debating society, which held weekly meetings. These activities, together with two contributions by Elisha Newton Plank to the *Horticulturalist* when he was about 26 years of age, show that he was thoroughly familiar with the flora of his community, was keenly interested in the discovery of attractive and useful plants or of any species new to his locality, and that the foundation for his career as a botanist may be traced back to an early period in his life. He set about to improve the old orchard on his father's farm by grafting, and planted an extensive young orchard, taking advantage of the best horticultural knowledge of his time. Thus, we find him spending his early manhood in Wolcott, living on his fruit farm close to the village and engaged in the practice of law.

During these years Plank promoted and participated in many civic enterprises of his community. He organized and promoted a local Agricultural Society. He was the prime mover in establishing the Leavenworth School, then a private school, as a tax supported public grade and high school. This was the first free public school in that section of New York, and required special legislative enactment. He served as president of the school's trustees for a period of fifteen years and for a time as mayor. During this period he was also active in promoting the building of railways in Wayne County, and served as attorney for the Ontario and Lake Shore Railway.

Plank had, therefore, led an active life and reached mature manhood before he moved with his family in 1879 to Independence, Montgomery County, Kansas and later to Wyandotte, now a part of Kansas City, Kansas. His interest in botany was doubtless stimulated by the new flora of the west, for he was soon occupied in a study of the native flora of Montgomery County. Failing health called for an out-of-door life and the study of the flora soon became his dominant interest. In 1880 he delivered a lecture on Kansas Forests and Forestry before the Kansas State Horti-

cultural Society, and he also contributed a paper in the Transactions of the Kansas Academy of Science in which he announced his project of a Flora of Montgomery County.

During his residence at Independence, we have reports of his activities as a correspondent of several newspapers, including the *South Kansas Tribune*, where he contributed a series of articles on the history of Montgomery County. He also contributed a series of articles describing his experiences and western travels to the *Lake Shore News* of Wolcott, New York.

In the years that followed, we find that Plank employed his ability as lecturer on botanical and kindred subjects on many occasions. He addressed the 14th Annual Meeting of the Kansas Academy of Science on the subject: "Botany popularly considered." He seems to have traveled extensively and served as lecturer on botanical and philosophical subjects over a period of nearly ten years in many communities of Kansas. He usually presented a series of five or six botanical lectures, which were given on week day evenings, with a lecture on Sunday evenings on some philosophical subject such as "Natural proofs of the immortality of the soul." These activities provided him with an income and contributed materially to the support of his family.

Several well known botanists can recall Plank's lectures during the eighties. To quote from a letter recently received from one of them:

"I saw Plank on one occasion only, when I was teaching the sciences in the Emporia, Kansas, High School. He was wanting to give a series of evening public lectures on flowers,² charging a nominal admission fee for the course. He wanted the free use of the high school and wanted me to introduce him around the town, vouch for him, help him sell tickets and be his publicity man.

"I liked him and did all that he asked. I had heard Snow, while I was a student, mention Plank's name with respect, and that gave me some assurance.

"Plank handled his subject from the aesthetic standpoint almost entirely, quoted poetry frequently, and really charmed his audience. I wrote an appreciative account of him for the newspapers and he seemed happy over the results."

From this communication we see that Plank used rare good judgment in providing his popular audiences with a type of lecture which was entertaining, held their interest and attention, and which was designed to create an appreciation of nature rather than to deliver a more technical discourse on botany.

Plank's activities took him to many new localities where he studied the flora, and we soon find him engaged in an ambitious enterprise visiting all parts of the state to collect specimens for a projected book on the Flora of Kansas. He would ship his baggage ahead to the next station, send his dried specimens back to his home in Kansas City, Kansas, and walk overland as he filled his plant press with new specimens, also collecting field notes in a series of notebooks. With a stopover here and there, during which he gave public lectures, he visited every county in Kansas and collected a herbarium variously estimated at between 6,000 and 10,000 sheets representing about 2,000 species and varieties of Kansas plants.³ He intended to write a flora of the state based entirely upon his own collections. This project was never completed. The Book on the Flora of Kansas needed financial support that was not forthcoming, and for this reason was never finished. Instead we find Plank enlarging his project to include a Botany of the Great Plains. His travels now took him to other states, and while he never published a Flora, the herbarium which he assembled during this period, consisting of about 3,000 sheets, was later acquired by the New York Botanical

² In the prospectus and always in printed notices, these were entitled "Popular Lectures in Botany."

³ Anonymous—Botany of Kansas. Feature article describing work of Prof. E. N. Plank, *Kansas City Star*, April 17, 1890.

Garden. It appears that there were practically no Kansas plants in the collection which went to New York. Thus, the disposition of Plank's Kansas collection remains doubtful. The collection of Texas plants were received unmounted and included at least 124 localities from which enough specimens were collected to warrant the printing of special locality labels. From his daughter, Mrs. E. M. Saunders of Chicago, we learn that the Kansas specimens had finally been mounted and labeled, and the impression of several members of the family had been that all of his collections went to the Smithsonian Institution. However, they do not appear to be among the Kansas collections now in the National Herbarium, nor are they found among any of the collections in the University of Kansas or the State Agricultural College at Manhattan. The Missouri Botanical Garden received some collections, in part as exchanges, including chiefly the plants he collected in Arkansas.

During the period of Plank's travels in Texas, he wrote an extensive series of articles on the Flora and Agriculture of Texas which were published in *Garden and Forest*. His last contribution which was on the Flora of Southwestern Arkansas, appeared in the *Plant World* in 1898 near the time when he moved his residence from Kansas City, Kansas, to make his home with one of his sons, E. N. Plank, Jr. at Decatur, Arkansas.

He was survived by two other sons, Albert Rose Plank of Decatur, Arkansas, and William H. Plank of Bentonville, Arkansas, and by a daughter, Ellen Maria (Mrs. Wm. L. Saunders), for many years librarian at the Blackstone Branch of the Chicago Public Library. Several other children died in infancy.

Plank was a man of culture, of keen intellect, and a man of rare ability as a platform lecturer. His scientific writings, as well as his journal, show that he employed an excellent literary style, was a well informed man of unusually high ideals, and very independent in thought and action. His library contained, aside from Pursh's flora, Gray's manual, and the standard works in systematic botany of his day, a complete set of Darwin's works, several editions of Shakespeare, together with other books on English literature, history and various philosophical subjects. Among his highly prized possessions were some rare old books by John Ray, Michela, and others.

Plank's collections of southwestern plants contain many specimens which constitute the earliest known locality record for the species. Among the type specimens collected by Plank are the following: *Asler subsessilis*, Burgess, Benton County, Arkansas; *Cyperus Plankii* Britton, Corrigan, Texas (1894); *Mesadenia similis* Small, Benton County, Arkansas; *Rynchospora Plankii* Britton, Benton County, Arkansas; *Solidago pendula* Small, Benton County, Arkansas; *Xanthoxalis texana* Small, Alva Texas (1894). There are doubtless many others. Plank first collected the pods of *Gleditsia texana* Sargent (now believed to be a natural hybrid) which led to the search for more material from which the species was named.⁴

Among the writings of Plank and other records bearing on his life the following may be listed:

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⁴ SARGENT, C. S.—E. N. Plank, biographic note as a footnote in *Sylva of North America* 13:13-14. 1902.

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Botanical notes from Texas, XXIV. Gar. & For. 8:72-73. Feb. 20, 1895.

Botanical notes from Texas, XXV. Gar. & For. 8:193. May 15, 1895.

A botanical journey in Texas, I. Gar. & For. 9:62-63. Feb. 12, 1896.

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DEPT. OF BOTANY,
UNIVERSITY OF ILLINOIS,
URBANA, ILL.

Notes and Discussion

Additions and Amendments to the International Rules of Botanical Nomenclature

LOUIS CUTTER WHEELER

ART. 2. Change sentence 4 to read: "They are always retroactive *except when expressly limited*:..."

Argument: This change is for the purpose of making this article consistent with the provisions of Articles 38, 39, 43, 45, and 66 which have limitations of time.

ART. 18. Recommendations, add: "When a name is proposed for conservation the type species should be stated for the name or names to be rejected as well as for the name to be conserved."

Argument: This is a mere matter of precision in the routine of proposing names for conservation. If the type of a name is not specified the application of the name is often dubious.

ART. 21. Note 2. Change to: "The application of *both* conserved and rejected names is determined by nomenclatural types, or by substitute-types where necessary or desirable."

Argument: Since, according to Art. 18, "The application of taxonomic groups is determined by means of nomenclatural types," Art. 21, Note 2 is an incomplete statement of a self-evident truth. As amended above the statement is complete.

ART. 21. Note 3, 2nd sentence, change to: "In the event of union or reunion with another group, the name to be retained is that of the group to which the larger number of species had been assigned prior to the conservation of either or any of the competing names."

Argument: The purpose of conservation of names is primarily to preserve established usage. As it now stands, Art 21, Note 3, requires the rejection of a large conserved genus as *Rhynchospora*¹ Vahl in favor of the much smaller *Dichromena* Michaux in the event that the two are united as done by Bückeler in *Linnaea* 37:525-643. 1871-1873, Kükenthal, *Bot. Jahrb.* 56: Beiblatt 125:16-20. 1921, and Macbride, *Field Mus. Pub. Bot.* 4:165. 1929, and op. cit. 13:295. 1936. The first two authors retained *Rhynchospora* in spite of the fact that *Dichromena* was earlier. The rule as amended is more likely to serve the interests of stability of nomenclature and fulfill the intent of conservation than the present wording of the Rule.

ART. 23. Appendix II. Add the two following well-known names to the list of *Nomina familiarum conservanda*: *Dichapetalaceae* and *Onagraceae*.

ART. 30. Two subdivisions of the same species, even if they are of different rank, cannot bear the same subdivisional epithet, unless they are based on the same type. Of the two homonymous subdivisions of one species the name of the later is illegitimate and to be rejected provided that the earlier were validly published. Names of subdivisions of a given species which include the type must be based on the type of the species.

Argument: Sentence 1 is unchanged. Sentence 2 is intended to be an unequivocal restatement of the original ambiguous wording. Sentence 3 is added in order to avoid having to use subdivisional names which, though based on another type, nevertheless include the type of the species. E.g., in my judgment, *Euphorbia Fendleri* T. & G. var.

¹ Conserved spelling.

dissimilis Payson in Bot. Gaz. 6:379. 1915, should be included under *E. Fendleri* var. *typica*, Bull. Torr. Bot. Club 63:444. 1936. It is highly probable that someone else may consider Payson's variety distinct enough to constitute a separate varietal entity. If the principle of priority is allowed to transcend the principle of the type method the subdivisional name including the type of a species may shift, according to the vagary of the individual, from a name based on the type of the species to one based on another type. *Euphorbia Fendleri* var. *typica* and *E. Fendleri* var. *dissimilis* are, according to Payson's interpretation, distinct, but according to my interpretation they are synonymous though the two types are opposite extremes of the complex. As Art. 30 now stands, according to my biological interpretation of the complex, it should bear the name *Euphorbia Fendleri* var. *dissimilis* which would include the type of *E. Fendleri* but not be based on it—a system which is basically inaccurate and confusing and defeats the purpose of Rec. XVIII.

ART. 36. Paragraph 1, delete: "or indelible autographs."

ART. 36. Paragraph 2, add: Through Dec. 31, 1941 publication by indelible autograph is accepted. Offer for sale of material which does not exist does not constitute publication.

Add Note: For purposes of this article handwritten material, even though produced by some process such as lithography, offset, or metallic etching is still considered autographic.

Argument: Publication by handwritten material is an abomination due to the often poor legibility and lack of uniformity. Also, due to the present general use of inks which are by no means indelible, few such attempts at publication would qualify as indelible and validity of publication in such cases is a matter of opinion as to the indelible quality of the ink employed. It might be well to provide that printing be indelible to be valid but that might becloud the issue. The use of typewritten copy reproduced by hectographing, a process employing permanent water-soluble ink, is a sure way to insure the ultimate oblivion of the supposed publication.—The beginning date of this provision is set far enough after the Botanical Congress of 1940 that all may learn of the measure before it becomes effective. The fact that this measure is not retroactive will avoid raising any question as to past autographic publications.

The purpose of the second sentence added to paragraph 2 is to prevent publication of names by deposition of a single copy in an institution such as the American Documentation Institute and the publication of a notice that copies will be made for a given price. This system, while admirable for making available basic data, will permit valid publication by the mere offering to make copies for sale. Since the making of copies depends entirely on orders, no copies may ever be made, yet such publication is now probably technically valid. The original copy is never offered for sale. Hence, unless this measure is passed, publication can probably be effected by merely offering to make copies, as well as by offering already existing copies for sale. Of course this measure in no way prejudices the customary procedure of offer for sale of existing copies which is the best method of establishing dates beyond question.

ART. 37. Paragraph 1.

A name of a taxonomic group is not validly published unless it is (1) both effectively published (see Art. 26), and (2) accompanied by a description of the group or by reference to a previously and effectively published description of it. A name proposed provisionally (*nomen provisorium, alternativum, seu eventuale*) in anticipation of the eventual acceptance of a given group, or of a particular circumscription, nomenclatural position, or rank of a given group, or merely mentioned incidentally, is not validly published.

ART. 37. Paragraph 2, change to: From Jan. 1, 1942 publication of names of vascular plants cannot be made by issue of a ticket, even with a diagnosis, with a herbarium specimen. Names of non-vascular cryptogams may be published by issue of a ticket bearing a printed diagnosis with a herbarium specimen.

Argument (Paragraph 1): This is essentially the original proposal from Proposals by British Botanists, 16. 1929. As passed at the Botanical Congress in 1935, eventual names were accepted as validly published. The distinction attempted there between eventual and provisional names is so vague as to be a constant source of confusion and debate. Furthermore, acceptance of either eventual or provisional names, if they be different, is in direct violation of Art. 16 which provides that "Each group... can bear only one valid name..." The case cited by Dr. Robyns, Zesde Internat. Bot. Congr. Proc. 1:364. 1936, of "*Cymbopogon Bequaerti* De Wild. nov. sp." and the simultaneously published alternative or eventual name "*Andropogon Bequaerti* De Wild. nom. nov." can be dealt with very simply. If a later author wishes to credit the second name to De Wildemann he is entirely at liberty to do so even though this proposal is adopted. The only point changed will be that it will be a later validation of an earlier name originally invalidly published, or better, it might be considered as a new combination based on *Cymbopogon Bequaerti* since that would be clearer and quite correct in the light of Art. 60 and the other procedure would not, since an illegitimate name is not to be taken into account for purposes of priority.

Argument (Paragraph 2): It is now possible to publish the name of a vascular (as well as non-vascular) plant by distribution of herbarium specimens with handwritten labels bearing diagnoses. In actual practice workers on vascular plants do not customarily use this form of publication even if the labels are printed. It would endlessly complicate bibliographical work if it were used. In the study of vascular plants sets of standard exsiccatae are not recognized as a form of publication. Such sets are recognized as means of publishing names of non-vascular plants and it seems advisable to officially recognize the difference in procedure.

ART. 41. Add: New combinations and new names made prior to Jan. 1, 1942 will be accepted if the basynym with its author is given, or if a definite bibliographical reference to the place of publication of the basynym is given. Beginning with Jan. 1, 1942 new combinations and new names are validly published only when both the basynym with its author and place of publication including page and date of publication are supplied.

Argument: Definite rules for judging the validity of new names and new combinations are needed and this supplies them. At present the Rules leave the validity of such changes to personal judgment for which there are no clearly defined precedents. This proposal might seem to create the possibility of creating endless new names if many new combinations and renamings provided with Latin diagnoses were adjudged improperly made. Perhaps it would have that effect nomenclaturally if authors were so slipshod as to carelessly propose these nomenclatural changes but there would be no taxonomic difficulty if any hint as to the basis of the name were given, for implication of identity is sufficient evidence to assume taxonomic identity and establish typification. The validity of nomenclatural changes made without actual bibliographic citation has been challenged by Fernald & Griscom, *Rhodora* 37:154, footnote 1. 1935, Fernald, *Rhodora* 39:309-310. 1937, and Ross, *J. Bot., Lond.* 76:342. 1938.

ART. 56. Add: In case of simultaneously published homonyms the first author definitely rejecting one in favor of the other fixes the usage. The above provisions operate only after the provisions of Art. 21, Note 3 have been satisfied.

Argument: First sentence: There is no provision in the Rules for disposal of taxonomically different, simultaneously published, homonyms. The principle is embodied in Art. 56 but the specific application is omitted. An example of such a case is *Tithymalus* Trew, *Herb. Blackwellianum, Centuria 2: Tab. 123. 1754*, and *Tithymalus* Miller, *Gard. Dict. abridged ed. 4, 3: Tithymalus. 1754*.

Second sentence: This amendment is proposed in order that Art. 56 may be consistent with the provisions of Art 21 in the event that the above-proposed amendments to that article are passed. In the event that that proposal is rejected this sentence is automatically withdrawn.

ART. 60: Add at the end of "(1)": An avowedly and actually superfluous name is forever illegitimate in any combination or rank and its type is automatically the type of the name for which it was substituted.

Examples: An avowedly superfluous name is one which is proposed with an available name cited in synonymy or with a reference citation to such a name. An example of a name shown to be superfluous by the citation of a reference leading to an available name is *Calystegia sepium* var. *rosea* Choisy, DC. Prod. 9:433. 1845, where "Bot. Mag. 2. 732" is cited. In this publication of 1804 there is the available name of the same rank: *Convolvulus sepium* var. *americanus*. An example of an avowedly but not actually superfluous name is *Pteretis* Raf., Amer. Monthly Mag. 2:268. 1818, which was substituted for *Struthiopteris* Willd. on the untenable ground that *Struthiopteris* was "abominable." But the generic name *Struthiopteris* had been employed by two authors prior to Willdenow, hence Rafinesque's name, though avowedly superfluous, was actually necessary.

Argument: This measure will definitely dispose of avowedly and actually superfluous names. At present it is a matter of opinion whether an avowedly and actually superfluous name is the same as the available name for which it was substituted. This amendment will fix the typification of these superfluous names and their interpretation will cease to be a matter of opinion. The precedent for this procedure was definitely accepted at the last Botanical Congress by the adoption of new combinations as valid regardless of application. (See Zesde Internat. Bot. Congr. Proc. 1:347-354. 1936. J. Bot., Lond. 74:76. 1936, & Kew Bull. 1936:186. 1936). Under the same theory avowedly and actually superfluous names are considered as mere renamings and if their diagnoses, if any, differ from the available name cited in synonymy it is considered a mere misapplication.

ART. 69: Examples: Change last sentence to read: This is treated, not as a new name, but as a new combination, *C. polyandra* (Hooker) Benth.

Argument: The wording of this sentence in ed. 3 of the Rules (1935) was: "This is treated, not as a new combination, but as a new name, *C. polyandra* Benth. (1863)." It seems obvious that validation by transfer does not create a new name either in fact or theory. The name used is the same and is based on the same type in both cases. In fact this sentence as it now stands violates Art. 49 requiring parenthetical authors for transferred names (it is sophistry to argue that validation by transfer is not a transfer) and the important principle, stated in the last sentence of Art. 54 "the citation in parenthesis (under Art. 49) of the name of the original author, _____, indicates the type of the epithet." Sprague, Zesde Internat. Bot. Congr. 1:351. 1936, very ably presented the relationship between the practice of the type method and the practice of citing original authors in parentheses.

In view of some of the past disastrous consequences of oral amendments to proposals before the botanical congress, it might be well to require that any amendments to measures proposed must be submitted in printed or typewritten form at least the day before the section on nomenclature meets. Formal proposals are now required to be submitted at least a year in advance of the Congress in the form of 100 or more printed copies. Fundamental changes without due consideration may be made by oral amendments, under the present system, to measures being considered. It is dangerous to allow oral amendment to be made. All amendments of any kind should be printed in advance so that they may be studied and their implications considered. To delete a portion of some measure often has disastrous effects, yet deletion of some controversial portion of a proposal may assure its passage and five years must pass before the damage can be rectified.

GRAY HERBARIUM, HARVARD UNIVERSITY,
CAMBRIDGE, MASSACHUSETTS, U. S. A.

Book Reviews

CONSERVATION IN THE UNITED STATES. By Members of the Faculty of Cornell University, A. F. Gustafson, Professor of Soil Technology; H. Ries, Professor of Geology; C. H. Guise, formerly Professor of Forest Management; W. J. Hamilton, Jr., Assistant Professor of Zoology. Comstock Publishing Company, Inc., Cornell Heights, Ithaca, N. Y. 1939. Price \$3.00. 9½ in. x 6½ in. Bound in green cloth. Pp. i-xi, 1-445. 232 figures, mostly half tones and a few maps and diagrams.

This well gotten together volume takes up the subject of conservation of the natural resources of the United States in practically all its aspects. It is divided into four parts, one by each of the authors: Conservation of Soil and Water Resources, by Gustafson; Conservation of Forests, Parks and Grazing Lands, by Guise; Conservation of Wild Life, by Hamilton; Conservation of Mineral Resources, by Ries. The different portions are well balanced starting from early history of the subject to modern conservation practices. The reviewer is glad to see so many pages, 257-346, devoted to the conservation of wild life, a field frequently neglected or slighted in favor of conservation of soils, forests and mineral resources.

That the work is intended primarily for students is indicated by the list of questions following each chapter. Copies of it should be in every laboratory where conservation is being taught and practised. It ought to have a wide distribution throughout the public libraries of the country, secondary schools and colleges, as well as such centers of conservation as the CCC camps.

The reviewer thinks that much of the optimism of the book is well justified, though he can scarcely have his attention drawn away from the cartoon frontispiece by Ding. After all, we can not have our cake and eat it, too. Conservation in many respects is a method of making the banquet last longer.

The book deals with a timely subject, and one which deserves everyone's attention. It is closed with a list of selected supplementary readings and a good index.

—M. W. LYON, JR.

THE SYNTHESIS OF SCIENCE AND RELIGION. By Frederick Kettner. The Biosophical Institute, New York, 1939. 22 pp.

This pamphlet by the founder of the "Biosophy" movement (whose patron-saint is Spinoza) is a well-intentioned but amateurish effort toward bridging the chasm between science and religion. To put it bluntly, it constitutes a rather feeble contribution to the already immense literature devoted to this problem of reconciliation between reason and faith, logic and revelation, science and theology. Only those who accept the pantheistic doctrines of Baruch Spinoza will be satisfied by this solution of the alleged dilemma and they might preferably consult the master's own writings instead of this meager exposition by a disciple.

To say that science is to religion as matter is to spirit, is an over-simplification which neglects the social or human sciences (pp. 6; 17). The "biosophers" are not speculative theologians but ethical technicians (p. 6). Again, "the essence of science (is) intuitive logic, and the essence of religion (is) integrative ethics" (p. 10). Religion must be creative and dynamic and the friendship motive must replace the motives of fear and hope for reward (p. 11). Freedom, liberation, intuition and integration are frequently repeated terms while prejudice and superstition would seem to be the chief evils cited. In conclusion, this tract is at once harmless and futile.—D. C. O'GRADY.

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